The Living Anatomy of the Digestive Tract of the Goat: a Radiological Study of the Postnatal Changes.

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Department of Anatomy
Royal Veterinary College
University of London

Thesis presented for the degree of
Doctor of Veterinary Medicine and Surgery

October, 1958

Vet. Lib.

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Summary

The anatomy and motor activities of the digestive organs were studied in fifty-two goats, aged between sixty hours and fourteen months. The animals were hand-reared and although provided with access to solid fodder from the first, continued to be fed a limited amount of milk beyond the usual time of weaning. The abdomen was dissected in ten animals embalmed in the standing position but, this apart, radiological methods were employed. In addition to single films, the movements were studied fluoroscopically and by serial radiography, great reliance being placed upon the latter as supplying an objective record. A number of cinefluoroscopic sequences were also obtained.

The radiological anatomy and the post-natal changes in topography are described and the details cannot conveniently be summarized. Development is rapid especially in the first six weeks and a virtually adult condition is reached by three months or thereabouts. The following are the principal observations on mechanics.

On deglutition, fluids may be temporarily arrested at three points en route to the stomach and may pass to and fro in the thorax before passing the cardia.

The rumen and reticulum develop rapidly after birth, especially between the second and sixth weeks. Both are active from the first weeks and an adult pattern of behaviour appears soon after the sixth week. The ruminoreticular activity never acquires great regularity and, in addition to the two-stage reticular and the two- or four-stage ruminal cycles commonly described, shows additional independant contractions of the major and blind sacs.

Growth of the omasum is retarded until considerable amounts of solid fodder are consumed. Its main activity is co-ordinated with reticular contraction when the upper pole dilates and fills: later this part contracts and the expulsion of food is assisted by constriction of the middle and distal sections. Alternating contractions and relaxations occur at other times also.

The abomasum determines the abdominal topography at birth but soon decreases in relative size. Its parts and activities resemble those of the simple stomach and both uninterrupted peristalsis and antral systole occur: the latter is regarded as a modification of the former and predominates during the first six weeks or so: later the movements are almost exclusively peristaltic. Activity is greatest between the second and sixth week.

The duodenal bulb exhibits systolic and other less clearly defined contractions. The remainder of the small intestine shows peristaltic, segmental and other activities in complex combination. Peristalsis predominates in the proximal, more active, part and gradually gives way to segmental activities when the intestine is traced distally.

The large bowel continues the gradient of activity. The caecum and colon show peristaltic and (proximally) antiperistaltic contractions in addition to several types of segmental contraction.

The results as a whole emphasise the precocious development of adult topography and behaviour and demonstrate the close integration of structure and function. It is suggested that the exclusive study of the dead animal leads to a misconception of the essential nature of visceral anatomy.

Preface

The literature describing the anatomy and mechanics of the digestive tract of the ruminants is so considerable that further investigation of the more fundamental aspects may appear redundant and the presentation of results unjustified unless they contain observations or interpretations that are strikingly novel. Since this distinction cannot be claimed on behalf of the present account it may be as well to indicate briefly the origin and purpose of the investigation it records.

A study of the radiological anatomy of the digestive organs of the dog jointly undertaken in this Department provided an introduction to the concept of fluid anatomy which stresses the inherent variability of the viscera. This approach to the study of these organs has attracted little notice among veterinary anatomists and our first impressions were so stimulating that it was resolved to extend the investigation, as circumstances permitted, to the other domestic species. The opportunity of making a limited study of the abomasum of the goat occurred in the following year and while this was necessarily curtailed when an outbreak of foot-and-mouth disease interrupted the supply of animals it demonstrated the practicability of applying radiological methods to the study of the ruminant abdomen and introduced us to some of the relevant literature. Thus we were made aware of the conflicting views which this contained and our notice was drawn to the unequal attention that has been paid to the various aspects of the subject. Much of the confusion and conflict appeared to stem from the variety of techniques and to the differences in species and age of the experimental subjects that had been used and it was believed that a general survey of the radiological anatomy and mechanics in the one species and including animals at different stages of development might be useful, particularly as the only review of these matters then available was incomplete and had appeared before the formulation of many of the modern theories and ideas pertaining to the subject.

Shortly after this decision was reached a combination of circumstances led to the breaking up of the team and after an interval the present writer resolved to continue with the project as an independant research. Greater familiarity with the literature made it clear that certain activities of the ruminant digestive system are adequately known and experience showed that others are not well adapted to study by radiological methods. For these reasons the original scheme has been modified and the scope of the investigation restricted in order to concentrate upon certain of the more promising aspects. Those to which most attention has been paid include: the comparison of visceral anatomy in the living animal and the dissection room subject: postnatal changes in abdominal topography: the activities of the omasum, abomasum and duodenum: and the onset of gastric activity and its modification in the growing animal.

In studying previous work on these and kindred topics the lack of objective confirmation of the authors' statements has often been apparent: this has been particularly evident when reference is made to fluoroscopic observations for these are notoriously liable to various interpretations and even when radiographs are included they depict but a single phase of activity. For this reason great stress has been laid upon securing serial radiographs and a fairly comprehensive selection of these has been reproduced in order to provide a source of reference for the conclusions which have been reached. Some of these sequences are believed to illustrate activities that have not previously been recorded while others contradict accepted views: but even when they support the common interpretation they are perhaps of utility in supplying a permanent record of the movements. Indeed throughout the account much of the burden of description has been placed upon the illustrations for they are both more succinct and more reliable than written comment.

The present appears to be an appropriate point at which to undertake the pleasant duty of acknowledging the assistance that has been received from numerous helpers. A work such as this requires at times the assistance of many hands and a special debt is owed to past and present colleagues, Messrs. F.S. Drury, R.H.A. Merlen and F.J. Wadsworth, who generously assisted at the radiological examinations. Willing co-operation has also been given by the technical staff of the Department and by the attendants charged with the care of the animals: special mention must be made of Mr. C.A. Fowler who has been responsible for most of the arduous Dark Room duty and for the reproduction of the majority of the illustrations. The assistance of the staff of the Department of Diagnostic Radiology, University College Hospital, London, who prepared the cine sequences is also much appreciated. As always the library staffs of this College, the Royal College of Veterinary Surgeons, the Wellcome Historical Medical Library and the Royal Society of Medicine have been most helpful. A special acknowledgement is due to Mrs. C. Millington who so ably dealt with a most untidy manuscript. Finally this opportunity is taken to thank Professor J. McCunn for his encouragement and for freely making available the facilities of his Department.

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Introduction.

Before proceeding to the descriptive part of this thesis a historical review of the development of present knowledge of the ruminant gastrointestinal tract may assist by placing the subject in better perspective: but since the accounts of the activities of the individual organs are preceded by a short preamble setting out the more important contributions this general survey may be held to brief extent.

The compound stomach of the ruminants early excited the curiosity and engaged the interest of naturalists. Aristotle appears to be the first whose writings on the subject have survived: he was fully aware of the unusual nature of this organ and he sought on several occasions to correlate its structure and function with the development of other parts of the digestive tract: his observations and conclusions were repeated in modified or distorted forms by Pliny, Galen and by many other writers of antiquity who themselves contributed little. All these accounts were of a relatively general nature: more exact descriptions awaited the investigations of the anatomists of the sixteenth and early seventeenth centuries, among whom Coiter and Fabricius are especially prominent in this connexion. Fabricius, in his treatise 'De gula, ventriculo, intestinis tractatus', 1618, gives a lengthy description of the

Ex Libris

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MERYCO-
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SIVE DE
RVMINANTIBVS
ET
RVMINATIONE
COMMENTARIVS.

Quo primùm exponuntur
*RVMINANTIVM SPECIES ET DIFFE-
rentiæ, per omnia animalium genera; deinde organorum
ruminationi inservientium admiranda structura detegitur, & iconibus
æri incisis ante oculos ponitur: denique de ruminatione ipsa
ejusque causis ac utilitate differitur.*

BASILEÆ,
Apud JOH. LUDOVICVM KOENIG
& JOH. BRANDMYLLERVM.
M DC LXXXV.

Fig. 1. Titlepage of Peyer's Merycologia, Basileae 1685.

anatomy and physiology of this organ, noting among other matters the differences in proportion of the gastric compartments in the adult and the newborn and commenting upon the role of the oesophageal groove, the 'via lactea', in the conveyance of milk to the abomasum of the sucking calf. Other observations on function are less happy and considered as a physiological exposition the account as a whole merits the criticism of Cole (1944) that it is largely speculative and adds little to previous knowledge. The same stricture may be applied to the physiological theories of Peyer, the author of the earliest *monograph on the subject 'Merycologia' which appeared in 1685 (fig.1). In this important work Peyer takes a broad view of his subject and in addition to the obvious topics he discusses phenomena in man and other non-ruminant species which he considers to be related to rumination. Much of Peyer's physiology is conjectural but his observations on anatomy are sound and are supported by excellent illustrations of which an example is reproduced here (fig. 9). Peyer lists close on two hundred authorities and while many of these are cited for their philological

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* The little known work of Aemilianus 'Naturalis de Ruminationibus et Ruminatione historia', 1558, has not been available. I am informed that the title is misleading and that little space is devoted to the peculiar processes of digestion in these animals.

opinions rather than for any real contributions to ruminant anatomy or physiology, the impressive total is none the less evidence of the age old interest in the subject.

Numerous other writers on ruminant anatomy, both before and after the time of Peyer, must be passed over without comment. The description of the gross anatomy of the stomach could be improved only in detail and exact accounts of the topography of this and other abdominal organs were impossible before satisfactory methods of embalming became available. Günther (1875) appears to have been the first to study this aspect of ruminant anatomy in properly hardened specimens and his account has been followed by many others. At the present time detailed descriptions of the anatomy of the digestive organs of the domestic ruminants are contained in the standard textbooks e.g. Ackerknecht (1943), Sisson (1953), May (1955) and Martin-Schauder (1938), the last named work providing most information on the more important features peculiar to the goat. There are in addition a very considerable number of specifically topographical studies: the most valuable of these are by Murphy, Aitkin & McNutt (1926), Lagerlof (1929), Schreiber (1953) and Nickel & Wilkens (1955) on the ox, Kolda (1930-1, 1931) and Wilkens (1956a) on the sheep and Andres (1928), Kolda and Wilkens (1956b) on the goat. A paper by Florentin (1953) is particularly concerned with the interconnexions of the various compartments.

Comparison of the results obtained in these investigations discloses considerable differences in detail even within the one species and there is good reason for believing that much of the contradiction is a consequence of faulty technique in the fixation of the animals. Lagerlof reviewed the earlier literature and examined the history, the scope and the limitations of the more common methods of preparation but further comment on this vital matter is better deferred until it may be re-examined in the light of the present enquiry.

The authorities so far quoted refer almost exclusively to the anatomy of the adult animal and remarkably little attention has been paid by modern anatomists to the immature stomach: indeed it is believed that until very recently Lagerlof was the only author to have studied the post-natal development on a topographical basis. Others quoted on this aspect, e.g. Auernheimer (1909), appear to have based their descriptions upon the study of the fresh viscera, a method which naturally gives little indication of the disposition of these parts in life. Hammond (1932) and Martin-Schauder give fuller references to this literature. Recent papers by Tamate (1957a, b) are specifically concerned with the development and growth of the stomach of the goat but in the main follow the traditional lines.

It is believed, however, that the weights and capacities of the various organs obtained in this way possess relatively little value since it is the content which determines the size and thus the relationships of each part and the activity which regulates its form. If this proposition is correct it follows that the viscera must be studied in the living subject. This approach to the study of the viscera of the human body was first advocated by radiologists who in the course of their work learnt to distrust and then to discount the traditional accounts of the anatomy of the abdomen: some were then stimulated to undertake the study of the viscera in healthy subjects and the results of their labours have made an important contribution to human anatomy. It is now universally accepted that the organs as they appear in the human cadaver may have little relevance to the conditions prevailing in life. The subject is well considered and fully documented in the monograph of Barclay (1936) who himself contributed extensively to the development of the modern views, perhaps not least by the coinage of the term 'Fluid Anatomy' which so vividly suggests the essential variability and mobility of the viscera. Although the conditions within the abdominal cavity of other species are very similar to those prevailing in man, comparable studies on the form and disposition of the abdominal organs of animals are exceedingly few in number and it may be said that the importance of this approach has received almost no recognition from veterinary anatomists. Even in 1956 a lengthy description of the effects of posture on the abdominal organs of the dog (Habermehl) appeared in which the agonal positions are described in detail and virtually no reference is made to the changes that incessantly take place in the living subject. Radiographic evidence is mentioned only to be rejected where it does not correspond with the cadaver.

No specifically anatomical study of the ruminant gastrointestinal tract undertaken by radiological means has appeared but much anatomical information can of course be obtained from studies of a more physiological intent, for whatever the failings of the radiographic approach it does at least serve to emphasise the essential unity of structure and function. Moreover quite apart from the textual comment many details of anatomy can be gleaned from the illustrations with which these papers are provided. These accounts will shortly be examined in more detail but immediate reference must be made to the works of Czepa & Stigler (1926, 1929), Phillipson (1939) and

Benzie & Phillipson (1957) for their importance in this connexion.

The physiology of the ruminant gastrointestinal tract has been studied by many workers and it is impracticable to consider all the publications, or even all of those devoted to the purely mechanical aspects. Fortunately excellent reviews of the subject to which reference may be made are available elsewhere: Hoflund (1940), McAnally & Phillipson (1944), Sporri (1951), Dukes (1955) and Habel (1956) may be specified. The text of Colin (1886) will also be found useful for its account of the earlier literature, particularly that of French origin.

It is usual to regard Flourens (1844) as the originator of the experimental study of the subject although in fact he was by no means the first in the field (see, for example, the review of Sporri). Flourens developed the technique which has later proved so fruitful and constructed fistulae leading from the exterior into the forechambers of the stomach: these provided access to the interior for visual inspection, palpation and for the introduction of test substances: in later hands they have provided a means of inserting and attaching balloons and other devices for the recording of the intraluminal pressures.

Among those who have developed this technique are Wester (1926), Schalk & Amadon (1928), Kryzwanek

& Quast (1937) and Phillipson (1939) and undoubtedly the basic knowledge of the movements of the rumen and reticulum is owed to the results obtained by these and other workers who used this method. It is difficult, however, to be easy in one's mind that the animal treated in this way is entirely normal if for no other reason than that the fixation of the organ to the abdominal wall is itself abnormal and must interfere in some degree at least with the freedom of movement which is so conspicuous a feature of all the viscera: the aphorism of German surgeons 'Wer viel pexiert, viel pecciert' quoted by Barclay in a different but similar connexion seems apposite. The detailed interpretation of the pressure readings obtained also appears to be fraught with the possibility of error particularly when attempts are made to compare the pressures within localised parts of the organ for, when the parts are in free communication, a change in one region must surely produce corresponding changes in the remainder of the cavity: and if the balloon is large enough to be gripped by the organ wall can there be certainty that it does not by its presence stimulate an unnatural reaction? Certainly it has this effect in the simple stomach. The modification of Quin & van der Wath (1939) who connected their recording apparatus directly to the fistula and then used the whole rumenoreticular sac as their 'balloon' is perhaps more reliable. Even so it is notorious that the readings obtained by these means are subject to distortion in many ways and while usually they may be accepted as giving a rough qualitative guide they are by no means accurate quantitatively: examples abound in other fields where the ingesta appeared to be proceeding in a direction which the pressure readings indicate to be movement from a region of low to one of high pressure, surely against the laws of nature. Quigley (1947) gives a penetrating analysis of the difficulties involved, entering deeply into the physics of the matter, and he indicates that while these difficulties may be overcome this requires a most complex technique and elaborate apparatus. These matters do not appear to have received critical attention in their relationship to the physiology of the ruminant stomach.

Another method that has been employed is the direct inspection of the exposed viscera in laparotomised animals following regional or general anaesthesia. This too has given valuable results (e.g. Mangold & Klein, 1927, Dukes & Sampson, 1937) but again is an animal exposed to these insults really in a normal condition? There can be no doubt of the answer. It may well be, probably often is the case, that the gastrointestinal movements that are seen in these animals correspond to those occurring naturally: but in such artificial conditions can one be sure? Certainly they sometimes give a distorted picture: Dukes & Sampson (1937) found that many of the movements they had described in animals with fistulae were absent in their other, laparotomised, subjects which in turn demonstrated a variety of contractions not seen in the former group. Much the same objection may be raised to the use of 'windows' - sheets of transparent material inserted in an opening of the abdominal wall produced by the resection of skin and muscle. Trautmann (1933a) is among those who have used this technique and while his results were generally similar to those he obtained by radiography, the method seems open to grave criticism. The replacement of part of the soft and flexible body wall by a sheet of solid material surely gravely impairs the normal state and must, one feels, be accompanied by pain and consequent inhibition of activity.

In a further technique the changes in electrical potential caused by the muscular contraction of the organ walls are recorded by means of a string galvanometer (e.g. Toman, 1928). According to Phillipson (1939) the results of these experiments must be discounted since the recordings are confused by the action potentials picked up from the abdominal wound.

These appear to be the main methods of investigation which have been employed in animals prepared by one sort of surgical assault or another: in indicating their scope they have been deliberately presented in a critical light - not because it is believed that the results they have given are useless or in the main wrong but rather because they relate so obviously to subjects altered in some way or other from the normal state that they must be regarded with suspicion and acceptance held in abeyance unless confirmation is obtained by other methods less unfavourable to the well-being of the animal.

First to be considered under this heading are the normal methods of clinical examination - palpation, auscultation and percussion. These are obviously restricted in their range but in the hands of the experienced diagnostician reveal more than might be imagined. They are, of course, most valuable in connexion with the more superficially placed organs, in this context, with the rumen and reticulum. By these means the position and extent of the parts and the sequence and to some extent the force of their contractions may be studied. Lagerlof (1929) and Williams (1955) are among those who have presented important studies using these methods, while Hoflund (1940) has provided a valuable check upon their accuracy by combining their use with palpation through a fistula. At this point brief mention may be made of a more recent and as yet less tried method of clinical investigation: the technique of peritoneoscopy involves the introduction of an endoscope through an incision made in the flank or vaginal wall and permits the inspection of the state and behaviour of the abdominal organs (Megale, Fincher & McEntee, 1956). But since the influx of air inevitably disturbs the equilibrium within the abdomen the method seems to have little value in physiological studies, whatever its ultimate place in clinical practice, since the same ends are obtainable with no greater disadvantage in a frank surgical approach.

The remaining method for the examination of the abdominal viscera is of course the radiographic, and since this forms the basis of the following account it may be examined at somewhat greater length. The application of X-rays to the study of gastro-intestinal activity followed rapidly upon their initial discovery. Some doubt concerns the priority of achievement in this field but perhaps the paper of Cannon (1898) is entitled to first place. At all events there was an early appreciation of the potentiality of the new technique and a succession of publications, rapidly becoming a flood, ensued and has persisted with relatively little abatement to the present time. Interest naturally centred upon the human organs and since much of the early work was conducted by radiologists the study of the normal was at first undertaken mainly to elucidate the pattern of disease in both its structural and functional aspects. But so great is the variation and so endless the diversity of activity that even now the full range of the normal is hardly known and new details continue to be recorded. Some of these papers will be noted in the appropriate context: general reviews of the subject are provided by Catel (1936), Barclay (1936) and Alvarez (1948) while a fully illustrated modern account of the normal appearances will be found in the monumental treatise of Schinz, Baensch, Friedl & Uehlinger (1954).

Although the clinicians have predominated in the production of this literature there has also been a considerable interest from physiologists who have extended their investigations to the study of the gastrointestinal tract of the laboratory species, and of the dog and cat in particular. The other domestic species have not gone unnoticed: Neimeier (1939) and Hartmann (1942) for example, have studied the gastrointestinal tract of the pig, while Müller (1951) and Hill (1952) have described the appearance and movements of the intestine, and of the whole tract respectively, of the horse. The monograph of Hill incidentally provides a valuable entry into the comparative literature. Alexander & Benzie (1951) give an account of the radiological anatomy and of the rate of transport of the ingesta in the foal which will have some relevance to the results of this enquiry.

But of the various farm animals most attention has been devoted to the ruminant either because of their particular economic importance or because of the unusual nature of the gastrointestinal tract and digestive processes in these animals. The first radiographic study of the alimentary tract of a ruminant was produced by Czepa and Stigler, the former a radiologist, the latter a physiologist. Their account appeared in two parts, in 1926 and 1929, and covered, or at least touched upon, almost every aspect of the movements of these organs. In their work Czepa and Stigler relied upon single radiographs and upon fluoroscopy, attempting to record the pictures presented by the latter technique in lightening sketches. Inevitably they appear to have allowed themselves to be mislead at times by the rapid course of events and some of their observations have since been proved wrong, while others have required elaboration and modification in the light of further knowledge: nonetheless this pioneer publication has remained the basis of all later studies and it must be recognised as constituting a very remarkable achievement.

Their first communication immediately stimulated interest in the application of radiographic technique to ruminant physiology and a succession of papers by other authors followed. Most of these confined their attentions to limited topics: Toman (1928), for example, studied the movements of the corumen: Magee (1932) the movements of all the compartments of the stomach: Trautmann (1933) the ruminal activities in the kid: Hagemeier (1937) the movements of the intestine, especially the caecum: Engl (1938) the course followed by solid ingesta: Phillipson (1939) once again, and in greater detail, the movements of the stomach: Hoflund (1940) the effects of nerve lesions on gastric motility: Sporri & Asher (1940) the movements of the large bowel: Watson & Jarret (1944) the oesophageal groove reflex and the course followed by fluids: Aleev (1952) the process of rumination: Dyce, Merlen & Wadsworth (1953) certain activities of the abomasum: Dougherty & Meredith (1955) and Dougherty & Habel (1955) the process of regurgitation, using for this programme the technique of cine fluoroscopy. Stigler himself published a later paper in 1929 in which he alaborated certain aspects. Others such as Duncan (1953) have used radiographic methods incidentally in the course of work relying mainly upon other techniques.

A more comprehensive study of the subject is provided by Benzie & Phillipson (1957) who recently published a monograph, in atlas form, illustrating most aspects of the movements of the stomach and intestine: unfortunately the accompanying text is very short.

There is thus a considerable body of work relating to the subject but it is rather unevenly distributed over the various aspects and the different species for all three of the domestic ruminants have been used in these studies, the ox naturally only in the first stages of its postnatal life; but little is known of the extent of species variations. Most attention has been paid to the movements of the rumen and reticulum and to the course taken by the meal on first ingestion while more recently the topics of eructation and rumination have received closest study: less is known of the omasum, which has been refractory to radiological investigation, and little notice has been taken of the abomasum which some seem to have regarded as comparatively inert. The intestines have also been neglected: apart from the original description of Czepa & Stigler only Hagemeier and Sporri & Asher have examined them at all and both of the last named papers referred almost exclusively to the large bowel. There is a notable paucity of work directed to the elucidation of the pattern of activity in the younger subject. Serial studies appear to have found a place in only one of the accounts mentioned although they have been found most useful in elucidating the nature of the movements in other species, e.g. Gianturco (1934a, b), MacLaren, Ardran & Sutcliffe (1950): the even more valuable cinefluoroscopic technique has recently found employment but little has as yet been published of the results obtained by the method.

Before proceeding to examine the utility of radiographic methods of examination it is necessary to consider their accuracy. It is of course true that, with the ordinary technique, opaque meal examinations depict only the interior of the organ and the boundaries of the images represent the contours of the mucosal layers with their various folds and, in certain cases, ornamentations. Nothing is revealed directly concerning the state of the other tunics of the organ wall. It is however customary to interpret alterations in the form of the mucosal outline in terms of the activities of the muscle of the wall and generally the propriety of this interpretation has not been questioned: indeed it forms one of the principal foundations for the clinical radiography practised in the human patient. The radiologist confidently interprets indentations flowing over the stomach towards the pylorus as representing the passage of peristaltic waves, and similar assumptions are made for the other organs and the remaining activities. Sometimes however it is necessary to bear in mind the possibility of confusing the movements of the muscularis propria with those of the muscularis mucosae: generally the amplitude and force of the contractions is sufficient to identify the more powerful waves as productions of the main muscle tunic but occasionally attempts are made to deny this solution and it is asserted that the muscularis mucosae produces these striking effects. There is however good evidence to the contrary: the usual solution accords well with the expectations raised by examination of the organ movements in the open abdomen while more recently an even more convincing demonstration has been provided by Pryde & Pendergrass (1954). These workers studied the movements of the antral region of the stomach in dogs which had been prepared not only by the administration of an opaque meal but also by the intraperitoneal injection of gas: in this way both the internal and external outlines of the wall were displayed and it was shown that the characteristic indentations of the barium shadow did in fact correspond to alterations of the external surface of the organ. The illustrations to this paper are very clear and leave no room for doubt and it seems permissible to give these results a more general application. Independant mucosal activities do occur but their discrimination, though not as a rule involving much difficulty, must be considered in the specific context of each organ.

It is still open to argument that the general representation of the organs does not correspond to their true appearance for the divergence of the rays naturally results in a certain distortion of the projected forms. This effect must certainly be taken into consideration: it is obviously most important when the organ is situated relatively far from the cassette for the degree of magnification is directly related to the relative distances between the source of the rays and the organ and between the organ and the film. Furthermore should the rays not be centred directly over the part undergoing examination there will be a certain distortion and in the periphery of the field the combination of these factors may produce apparent translations in position of organs lying at different levels. Normally one is on guard against these artefacts and the effects can, of course, be minimised by careful attention to technique. They cannot be entirely eliminated but while they are obviously of importance in determining the anatomical relationships they are negligible in the study of the function of the parts. Most texts of radiodiagnosis, e.g. Barclay or Schinz et al carry full discussions of these points.

Another defect, also of importance in determining the topography of the abdomen lies in the inability to visualise all the contents of this cavity. Some organs possess a contrast so little different from the surrounding parts that they never appear in radiographs - for example the fat which is usually present in generous quantities in the ruminants and occupies a not inconsiderable space. Others such as the kidneys present a poor contrast and while they may appear without special means being taken the demonstration is normally poor and is naturally not assisted by the barium meal: and of course those organs which are outlined by the opaque meal are also shown only when they are actually filled with this material and are invisible at other times; much of the small intestine falls into this category since it is intermittently filled and therefore displayed. It is, of course, possible to determine something of the position of all these parts by noting the restrictions that limit the extension of those other organs that are more easily studied. There are also available certain special procedures that may be applied to the portrayal of individual viscera.

Another drawback which is perhaps of even greater consequence consists of the inability of normal radiographic methods to show the organ in 'the round'. The impression is necessarily two dimensional for since many of the parts are constantly in movement it is impossible to study them in a single phase of activity by means of simultaneous stereoscopic or multi-angle views without the aid of the most elaborate equipment.

These restrictions on the value of the radiographic technique are believed to be of relatively minor importance and it is hoped to demonstrate this in the general discussion. Of more immediate relevance to the exploitation of the technique for physiological purposes is the question "Admitting the accuracy of the radiographic evidence, what information does it provide?" The radiograph shows the position at a given moment, or if series are taken and the screen used, the sequence of events is made clear, but it reveals nothing of the underlying causes which produce the activities and which effect the movement of the digesta from one place within the tract to another. It is then clear that the method can only provide the basic information concerning the normal processes and while for this purpose it is probably superior to any alternative technique, alone it will not demonstrate the underlying nervous, chemical or humoral control of the digestive organs. If this restriction is accepted the application of radiography to comparative gastrointestinal physiology has full justification and ample scope for use and will rarely fail to produce the necessary foundation for later more exact work. The appreciation of Rowlands (1953) arrives at a similar verdict.

Wester (1930) alone appears to consider radiography unphysiological but his arguments hardly require refutal since the polemics with which he argues his case against the work of Czepa & Stigler reveal the weakness of his ground. Perhaps the sole point on which a specific rebuttal is indicated is that concerning the possible effects of the opaque medium: the materials now available are certainly inert chemically and are compatible and mix well with the usual foodstuffs and whatever the effect of pure aqueous suspensions there is no reason to suppose that the stomach and bowel react to their presence other than in the usual manner when they are given combined with the normal feeds.

Materials and Methods.

This enquiry extended over the years 1952-1957 during which time fifty-two goats were examined: these ranged in age from one-and-a-half days to fourteen months. Six of the animals were studied intensively and were re-examined at intervals throughout the first six months of life: the remainder were employed as circumstances permitted and in many cases were available on only the one occasion, being thereafter required for the purpose of class dissection. The latter was the ultimate fate of most of the kids but ten, of different ages, were set aside for post mortem examination in connexion with this study: these were preserved in the standing position and especial care was taken to minimise disturbance to the topography of the abdomen during the processes of slaughter and embalming. The general technique of preparation of these specimens was that advocated by Kolda (1931) and the organs were studied in situ by stripping of the flanks. A proposal to record the weights and capacities of the fresh organs of a further series was soon abandoned as being wasteful of animals and unlikely to yield information of value.

The animals were supplied by several agents and were of both sexes and of very varied pedigree. Many were received within a few days of birth and this group furnished the kids used for intensive study. Others were obtained at ages ranging from one to four weeks and the exact date of their birth was not always known: it is believed that the maximum error in no case exceeded seven days and observations on these kids were delayed for some time to reduce the importance of this uncertainty.

The early history of some of the kids was thus unknown but when in our care all were maintained in a standard manner, modified only in the case of the small group intended to provide the subject of a special investigation. The system of management of the animals was admittedly far from ideal but was the best that could be contrived with the facilities available. Groups of about half-a-dozen kids, approximately equal in size and age, were housed in loose-boxes in which they were bedded on straw. At first the animals were bottle-fed on cow milk since goat milk was rarely available; the milk was supplied in quantities and in number of feeds suited to each kid. Initially four feeds were given at 8.30 a.m., 12 noon, 3.30 p.m. and 7 p.m. but the number was reduced to three, two and eventually one as the animals gradually became accustomed to solid foodstuffs. The single milk feed was, however, retained for so long a time as the kids were willing to such, a period ranging from eight to twenty-odd weeks since the retention of this habit facilitated the administration of the contrast meal and allowed examination of the abomasum unobscured by ruminal shadows. In addition to the milk feed all the animals, including the youngest, had permanent access to water and hay while concentrates and green food were also supplied. Considerable quantities of this fodder were eaten from a very early age but no attempt was made to record the amounts consumed by the individual animals. Occasionally the opportunity of penning the animals out of doors for a day presented itself and this provided them with their only experience of grazing.

Four animals were set aside to be reared on a wholly milk diet, with the addition of a mineral and vitamin supplement ('minadex', Glaxo Laboratories): unfortunately these kids became afflicted with coccidiosis at a comparatively early age and as only two survived for any time no more than passing reference is made to the observations they supplied.

The experimental meal consisted of a suspension of barium sulphate in water or milk. In the first year's work a laboratory preparation of the salt was employed but this had a tendency to settle from suspension on occasion, a circumstance which hampered the investigation and in particular the determination of the rate of passage of the meal through the digestive tract. In the following years Damancy 'Micropaque' , a preparation marketed as a radio-opaque medium for clinical use, was substituted and the difficulty overcome. The experimental feed usually consisted of a 20% v/v mixture of 'Micropaque' in milk and was given by feeding-bottle; it was generally willingly consumed. On a few occasions it reached all four chambers of the stomach and surprisingly this happening did not appear to be correlated with the age of the animal or with any unwillingness to such. Normally however a milk feed passes via the oesophageal groove and sulcus omasi to the abomasum and when it was desired to study the fore-chambers of the stomach an aqueous suspension of the agent was administered by stomach tube which delivered it to the ruminoreticular sac. The use of the tube was unavoidable as the goats would not readily consume a solid meal in which a sufficient quantity of the contrast agent was mixed. Fortunately the passage of the tube was a simple matter and appeared to cause remarkably little resentment. The point is stressed as later reference will be made to the influence of psychic factors on gastro-intestinal motility.

The apparatus available for the radiological examinations consisted of a Dean's mobile X-ray unit providing a maximum of 100 Ma for 0.5 sec. exposure at 70 pKv, 60 Ma for 5 secs. at 90 pKv; the maximum screening output was 3 Ma at 85 pKv. This machine was used in conjunction with a Potter-Bucky table or with a simple cassette stand. In the early years no special facilities for screening or for serial radiography were available and the arrangements were improvised: screening was then mainly conducted with the animal recumbent upon a 'Perspex' window inlaid in a wooden table and the screen was viewed from above: serial radiographs were obtained by the passage of cassettes below the false top of another table roughly modified for this purpose. This second table was covered in lead-rubber in which a window, of adjustable dimensions, permitted the passage of the rays and it was thus possible to secure a series of exposures of small fields on a single cassette: relatively extensive runs were obtained using a number of cassettes. After considerable rehearsal of the team required for feeding, moving and receiving the films and operating the machine it was possible to synchronise the various operations and series of 6-48 frames were exposed within relatively short times, a more rapid succession naturally being possible with the shorter sequences. Individual timing of each exposure was impossible but on smooth runs a calculation based on the total time of the series gave a

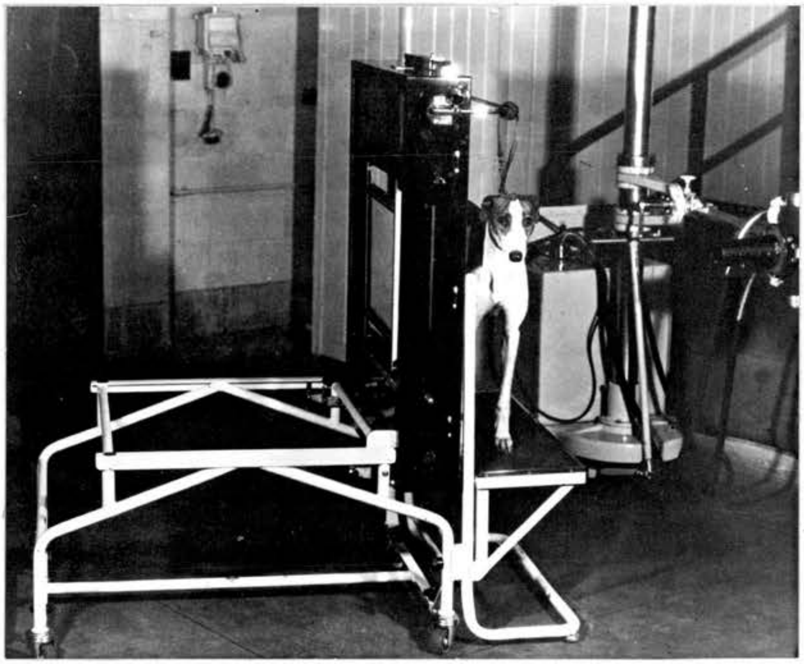

Fig. 2. A general view of the apparatus. A dog stands in the position of the experimental subject. The platform on which it is placed is adjustable in height and may be raised to bring any part in line with the s pace left uncovered by the shutters. The fluorescent screen is seen at the rear of the table which is lead lined, except for the adjustable central window, and provides protection to the viewer.

pretty accurate estimate of the intervals. Series in which there was some interruption were discarded save for anatomical study. Unfortunately exact registration of the position of the cassette for each exposure was impossible and movement and overlapping of the fields mar individual frames in many of the series.

Later a special table was designed and constructed to our specification by Messrs. Cuthbert Andrews (figs. 2 and 3). This table could be used in both the vertical and horizontal positions and it incorporated a fluorescent screen and a channel for the rapid passage and exchange of cassettes: the table top was covered in lead save for a window guarded by a system of adjustable shutters and provided convenient protection to the viewer and operator. When used for serial radiography the cassettes were contained in trays which were fed in and propelled by hand; when they reached the appropriate position they were automatically arrested by an electro-magnetic device which activated the tube, whereupon the cassette was immediately released and permitted to move forward once more. Continual pressure resulted in the successive exposure of predetermined areas on the films. Speeds of up to three exposures per second could be obtained on short runs without undue difficulty, but unfortunately the

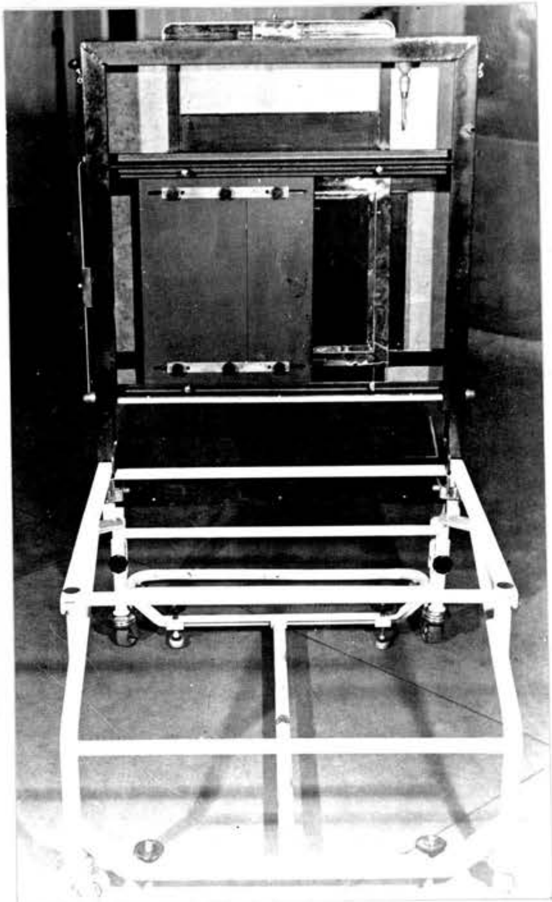

Fig. 3. View of the serial and screening table from behind. The apparatus is arranged for the study of the standing animal: for use with recumbent subjects the whole top may be lowered on to the frame shown. A cassette tray is in position (towards the left) and behind this may be seen a grid which may be removed when desired. The fluorescent screen has been taken away in order to display the other features.

noise associated with the action of the electromagnetic switch made it possible to use the equipment only with the more phlegmatic and experienced animals.

Since no special principles were involved other than those that govern animal radiography generally no remarks are necessary concerning the selection or processing of the films or upon the exposure technique. It will be only too apparent from the quality of the illustrations that the older animals taxed the resources of the apparatus beyond the useful limit. Work with the larger subjects was mainly confined to the procuring of single films since the longer exposure times necessary precluded attempts at obtaining rapid series.

Three radiological procedures were thus available and as they were used in various combinations on different occasions no single routine can be described as typical. In general the techniques were used in the following way: single radiographs were exposed at intervals to record the anatomy of the organs and the passage of the meal. These films were obtained in both the standing and recumbent positions, the former giving the best evidence of topography while the latter frequently permitting a more detailed visualisation of specific parts. Fluoroscopy was employed in the study of the activ-

Fig. 4 The oesophagus has been displayed as it runs through the neck and chest. The portion of the aorta that overlays this organ has been removed and reveals an indentation of the wall. The dimensions of the various sections of the oesophagus in the cadaver are not an accurate guide to the proportionate size of the parts in life.

ity of the various organs since it gives an appreciation of the movements that is not otherwise achievable; but as the impressions received in this way are liable to distortion by subjective influences confirmatory serial radiographs were obtained whenever possible to provide a very necessary check on this tendency and also to supply a permanent record of the movements. It is fortunate that many of the gastro-intestinal activities are relatively sluggish in execution and frames exposed at intervals of one to two seconds - in extreme cases $\frac{1}{8}$-4 seconds - provided a fairly satisfactory if incomplete record of most events for later detailed scrutiny. The use made of serial exposures was restricted however by several factors, of which the strain on the tube, the consumption of film and the radiation hazard were the most significant.

The facilities so far described were available within the department. The investigation was additionally assisted by the provision in 1953 of occasional access to the cine-fluoroscopic unit of the Department of Diagnostic Radiology, University College Hospital, London. A combination of circumstances made it possible to secure only a few short runs with this machine and these unfortunately were not always of particularly interesting phases of activity. Most of the cine sequences were of eight seconds duration and the frames were exposed at the rate of $12\frac{1}{2}$ sec.; they include brief glimpses of oesophageal, reticular and omasal activity and they have been studied by continuous loop projection in normal and slow motion. Extracts of these records are presented later.

The radiation danger is obviously of the greatest importance and every effort was made to minimise the risk to the laboratory personnel who wore protective clothing at all times. The fastest film and screens and the most restricted fields of exposure were employed to reduce the primary and secondary radiation respectively, and, in fact, the measures generally adopted were those advocated at greater length in a recent review (Dyce & Hawkins 1956), the single exception being the impossibility of having recourse to anaesthesia to immobilise the subject. No attempt has been made to assess the radiation received by the animals although in some cases it must have amounted to a considerable total, several goats being repeatedly used for screening, serial and cine work: none exhibited the least sign of any adverse effect. Benzie & Phillipson (1957) report much the same of their animals and present figures of the actual doses they administered which suggest that ruminants possess a considerable resistance to the effects of radiation.

In a previous short report (Dyce, Merlen & Wadsworth, 1953) brief mention was made of the care required to avoid emotional disturbance to the animals and evidence of the effect of such disturbance was put forward. This aspect is also noted by Benzie & Phillipson and others working with different species, e.g. Pascucci (cited after Golden, 1950) have reported specific indications of emotional modifications of the normal pattern of activity. The effects of emotion on the form and mobility of the human viscera are of course well known: graphic accounts are given by Barclay (1936) and by Todd (1930) among many others. In order to avoid or at least reduce the influence of these factors the animals used in these experiments were restrained as little as possible and between exposures they were allowed to run freely with their companions in the X-ray room. They rapidly became accustomed to standing or lying before the apparatus and to the darkness necessary for fluoroscopy and their behaviour suggested that except occasionally they felt little resentment of the procedures to which they were subjected.

A complete description of every examination was recorded in the day-book and this included an account of the observations made during each screening session prepared immediately this was concluded. Each film was identified by a number which indicated the animal and the date, sequence and time of the exposure. Certain of these figures appear on the reproductions and attention is drawn to them since it is possible that in certain circumstances they may give rise to confusion if there appears a contradiction between the figures and the legends: in explanation it may be stated that the animals of each year's work were numbered afresh and that in the series the cassettes and not the individual frames were marked at the time of the exposure.

Since present usage is by no means uniform the convention employed in designating the views may be mentioned. This defines the relationship of the animal to the film: for example, a right lateral view is one in which the right flank of the subject is nearest the cassette and the rays pass through its body from left to right. Thus in the ventral view the organs appear as they would in an animal regarded from above.

A number of subsidiary techniques of restricted application are noted in the appropriate context.

Observations.

In presenting the results of this investigation it has appeared most convenient to consider each organ or organ group in turn and so far as possible a uniform scheme of description has been adopted. An account of the radiological appearance in the mature animal is first given and this is followed by a description of the postnatal changes in topography. Motility is considered separately although a rigid division of the anatomical and mechanical aspects is of course impossible: this section is introduced by a brief description of the published work on the subject and it is concluded by a discussion which attempts to relate the present observations to previous knowledge and opinion. Consideration of certain matters which affect several viscera equally is reserved for a final general discussion.

Wherever possible the illustrations are located in relation to the relevant part of the text but it has been found necessary to relegate certain of the series to an appendix. A guide to the position of the illustrations will be found inside the back cover.

The abdominal parietes.

Of the various boundaries of the abdomen the roof and pelvic inlet are least affected by age and intrinsic activity. The roof is furnished by the spine and sublumbar musculature and since the latter is not especially well developed in this species, there is, in the lateral view, a relatively narrow gap separating the outlines of the bones from those of the viscera. In the standing position the normal lumbar spine is almost horizontal and where there are no fluid levels to guide orientation deviation from this appearance will indicate the extent to which the position is distorted. The line of the pelvic inlet is of arbitrary distinction and extends from the sacral promontory to the pecten of the pubis: the organs with which this account is concerned do not normally trespass beyond this limit.

The abdominal floor is more variable. In the youngest animals it continues the line of the sternum and it shows little ventral deflection when it loses the support of the xiphoid cartilage. In older individuals it is protuberant and becomes increasingly so with the increase in size and weight of the forechambers of the stomach: an accompanying change involves the ascent to the pelvic brim of the posterior part of the floor. This rises gradually in the newborn but becomes almost vertical in the adult (compare figures 15 and 29). The position of the umbilicus is indicated for some time after birth by the remains of the cord which attach to the skin. In several of the animals an opening in the muscular wall, the umbilical foramen, persisted for a while at this level and permitted the partial hernation of the abdominal organs, usually the lax walled abomasum. The effect was most marked during struggling or bleating or in other activities that increased the intra-abdominal pressure (see frame 21, plate 7).

At first the trunk is tubular, the lateral walls merging smoothly with the abdominal floor and continuing the line of the costal arch, but a change, similar to that involving the floor, soon affects the flanks and by six weeks or thereabouts these bulge outward considerably beyond the costal margin. A simultaneous increase in the transverse diameter of the intra-thoracic portion of the abdomen assists in producing a general widening of the trunk. These changes are associated with the development of paralumbar fossae or concavities of the upper part of the flank, features that cannot be discerned in radiographs.

The diaphragm completes the boundaries of the abdomen. It is difficult to obtain an accurate indication of the form of this structure and its exact radiographic study is beset with difficulties, associated in particular with the need for precise positioning: ideally steroscopic views must be obtained in the various phases of respiration but these require complex installations. It was not possible in this study to take the necessary precautions and the description is therefore very general. The radiographs (e.g. figs. 21 and 29) show that the upper part of the diaphragm is flattened and slopes downward and forward from the thoracolumbar junction to the point where the caval vein passes into the thorax: below this it is strongly arched and curves downwards and backwards towards the last sternebra. The most anterior part lies at the level of the sixth intercostal space tending towards the sixth or seventh rib according to the phase of respiration. It should be noted that the contour of the upper part is double as separate outlines indicate the right and left cupolae: of the two the left is the more anterior. Between these projections there lies a median recess resulting from the attachment of the crura to the lumbar spine. The costal insertions of the diaphragm are not shown in the radiographs. In younger animals the upper part of the diaphragm is flatter and does not project so far into the thorax as it does in the older goats: the condition in the latter is doubtless associated with the increase in volume of the abdominal contents, notably of the stomach. In the goat both abdominal and costal forms of respiratory movement occur although the former predominates in the resting animal. Neither appears to be sufficiently extensive to affect the abdominal topography in marked degree and it is hoped that the changes due to the respiratory excursions can be ignored without too great a loss of accuracy.

The Oesophagus.

In normal circumstances the oesophagus is invisible in radiographs and even during the deglutition of an opaque meal it is not occupied by a continuous column of ingesta. It is thus impossible to study the entire organ simultaneously but an idea of its radiological anatomy may be obtained from fluoroscopic observation and by the study of a number of plates showing different parts and the various phases of activity. It is possible to recognise by these means a number of regions which are distinguished by constant or recurring peculiarities.

The oesophagus (fig. 4) takes origin from the pharynx and is commonly regarded as extending caudally from the posterior limit of the cricopharyngeus muscle. There are however several features which cast doubt upon the utility of this interpretation. In the first place the posterior part of the pharynx, the segment corresponding to the cricopharyngeal muscle, is normally closed except during deglutition and this region, which has been designated, in the dog, the vestibule of the oesophagus (Zietschmann, 1939) or, in man, the oesophagopharynx (Evans, 1944) resembles the oesophagus in this respect. Furthermore on closer inspection the

Fig. 5 This exposure was made while the kid was sucking barium milk from a feeding bottle. The constrictions in the region of the cricopharyngeus muscle and at the thoracic inlet are conspicuous. An air bubble precedes the milk in the thorax.
The animal was aged 5 weeks.

constrictor fibres which are responsible for this obliteration of the pharyngeal lumen are found to be continuous with the circular fibres that embrace the first part of the gullet: Dougherty & Habel (1955) regard the whole formation as constituting a cranial oesophageal sphincter. The more usual elliptical or spiral arrangement of the oesophageal muscle does not commence until some way down the neck. The lumen of the upper cervical oesophagus is also rather narrow and even during the passage of ingesta remains considerably less wide than that of the succeeding part. The stretch of the oesophagus which lies below the axis is further distinguished by its asymmetrical appearance (fig. 5) for while the ventral border has a regular outline the dorsal margin is strongly indented: dissection reveals no external cause for this compression and it seems probable that the narrowing is produced by the contraction of those muscle fibres which, arising on the laryngeal cartilages, extend obliquely backwards to meet their fellows of the opposite side in the dorsal midline. Apparently such a development is peculiar to the goat among the domestic ruminants (Helm, 1907).

The greater part of the cervical oesophagus presents no particular feature: it lies in a rather variable position dorsolateral to the trachea on the left side and continues over the thymus and through

6

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Fig. 6. The subject was fed from a bottle. The exit from the oesophagus is sealed and the phrenic ampulla dilated. The size of this part, the obliquity of its base and the absence of a 'diaphragmatic' sphincter will be noted.

Fig. 7. This radiograph was obtained on a separate occasion. The bulb is much narrower when it is not closed distally. A constriction at the level of the diaphragm is probably produced by this organ: beyond this lies the oesophageal groove, slightly wider than the foregoing, and the omasum which is barely distinguishable. A quantity of the meal has already reached the abomasum.

the thoracic inlet in this location. A relatively extensive constriction affects the lumen to either side of the first rib and this part is also characterised by an oblique furrow passing forwards and upwards which in radiographs imparts to the organ a characteristic twisted appearance. It is suggested that this effect is produced by the pressure of the vessels proceeding into the neck.

Behind this point the oesophagus gradually opens out and when it contains opaque food it is quite clear that the calibre of the thoracic part exceeds that of the cervical, a point in direct contradiction of the view formed from the study of embalmed specimens (Rubeli, 1890). Within the mediastinum the oesophagus climbs onto the dorsal surface of the trachea and it continues back at a gradually increasing distance from the spine. In the dissected specimen, the oesophagus is strongly indented by the aorta, to the right of which it passes, but the indentation or deflection at this level is rarely evident in radiographs. The final part of the oesophagus inclines ventrally and thus it meets the slope of the diaphragm less acutely than would otherwise be the case. This last part is commonly expanded when it contains stationary ingesta and forms the phrenic bulb or ampulla: this appears to terminate by flattening against the diaphragm (fig. 6).

There is no radiographic evidence for the permanent existence of a sphincter on that part of the oesophagus immediately before the diaphragm although, as will be evident later, a constriction does appear about this point during certain phases of activity. On the other hand, when a continuous stream of food connects the oesophagus and the stomach there is a very pronounced narrowing of the lumen joining the base of the phrenic ampulla to the image of the stomach: this appears to coincide in position with the level of the diaphragmatic crura and suggests a sphincteric action of these muscles much more strongly than it does a narrowing at the true cardia (fig.7). The dissection of the cadaver supports this interpretation for in the preserved animal the oesophagus is strongly compressed as it passes through the hiatus in the diaphragm: but whatever its cause the constriction undoubtedly represents a physiological barrier.

Oesophageal Motility.

Previous literature.

The literature on the swallowing act and on the passage of food through the oesophagus is extensive but contains few references to the ruminants. The first radiographic study of the process was presented by Cannon & Moser (1898): They described a squirting of the more fluid material across the pharynx and through the first part of the oesophagus, the food being propelled by the voluntary contraction of the mylohyoid muscles: where this action is impossible for anatomical (bird) or experimental (section of nerve to mylohyoids) reasons the head is elevated in order to obtain the assistance of gravity. The further transport of more fluid material may be assisted by active peristalsis and this is certainly necessary for the movement of solids. Palugay (1927 gave a full account of the process and discusses the relative importance of gravity, peristalsis and of the initial impetus. It is certain that there are important specific variations (Hill, 1952).

The passage of food through the cardia forms a separate problem and the factors concerned are not yet clearly understood. Fulde (1934) has described, largely upon the basis of radiographic studies in man, three barriers which the food must pass in succession: the first lies above the diaphragm, the second at the level of this organ while the third is formed by a mucous membrane fold or valve guarding the entrance to the stomach. He indicated the passage of food into the stomach as occurring in this way: relaxation of the first sphincter allows a filling of the distal segment of the oesophagus as the diaphragm descends in inspiration: the topmost sphincter is now closed and as the diaphragm rises during expiration the trapped ingesta are drawn into the stomach by the expansion of the abdomen. The mucosal valve prevents reflux of the gastric contents. Others described quite different mechanisms and a milking action of the diaphragm is commonly suggested. In man at least, this last may be discounted since on direct palpation of the exposed crura Dornhorst, Harrison and Pierce (1954) found no pressure exerted on the oesophagus. On the whole recent work has tended to increase the importance attached to the valvular action of the mucosa and to diminish that attached to the sphincters. It is clear that there are important variations in different animals: for example the strong cardiac sphincter of the horse strongly contrasts with the weak muscular development of this region in the domestic ruminants and these anatomical distinctions must have a profound influence on the physiology of the part. Barclay (1936), Alvarez (1948), Hill and James (1958) may be consulted for fuller accounts.

Observations on the ruminant are equally conflicting. Czepa and Stigler (1929) reported the behaviour of the oesophagus of the goat during deglutition. They remark the very rapid passage of fluids in this animal and emphasise the cylindrical (as opposed to conical) form of the distal segment. They believe that two obstructions exist at the lower end of the oesophagus: one at the oesophageal hiatus, the other corresponding to the true cardia. They were unable to differentiate these locations by radiographic means. Experiments in which an opaque solid was introduced to the part of the oesophagus lying immediately before the diaphragm induced them to believe that the entrance to the stomach is normally closed but opens reflexly when a swallowing movement is initiated. The same conclusion was reached by Hill, studying the horse. Others, e.g. Aggazzotti (1910) believe that the cardia is normally open or closed only by the loose application of the oesophageal walls. Benzie & Phillipson reported that milk passes through the gullet in a continuous stream in lambs and kids but in successive gouts in the calf. Barclay, Alvarez & Hill provide extensive references to all but the most recent literature.

Observations.

Observations on deglutition were confined to the examination of the consumption of opaque milk, taken from the feeding bottle. For the most part kids aged two to five weeks were examined, sometimes in the standing position and at other times laterally recumbent. Attempts to record movements by means of serial radiography met with little success since the progress of the milk is very rapid and a continuous record is not obtained. Furthermore when several boluses are in movement simultaneously they cannot be confidently identified in successive plates. A cine fluoroscopic sequence was also obtained which shows the activity of the thoracic oesophagus in a rather older animal: an extract from this is reproduced (fig. 8, plate 1).

When the kids feed from a bottle the quantities they obtain with each sucking movement vary considerably: a number of factors affect this, the size of the aperture in the teat, the appetite of the animal and its individual skill being obviously concerned. In addition the gouts become progressively smaller during the course of the meal even when the greed of the kid is undiminished and apparently they experience more difficulty in obtaining the milk as the quantity remaining in the bottle decreases. Large gouts are immediately projected into the oesophagus but later in the meal the kid usually swallows less frequently and the smaller quantities are collected in the back of the mouth until they are passed en masse. The mechanics of this movement are not easily studied but presumably a sudden contraction of the mylohoid muscles is involved as in other species. Most often the bolus - the term is convenient if inappropriate - passes rapidly across the pharynx and through the first part of the oesophagus slowing as it reaches the base of the neck and often halting in the region of constriction that extends on either side of the thoracic inlet. Here it may remain until it is joined by later mouthfuls and eventually a continuous column may fill the lower two-thirds of the cervical eosophagus. A similar fusion of successive gouts was observed in this region by Hill.

When movement recommences, or if it is uninterrupted, the progress through the thoracic oesophagus is usually very rapid and on reaching the diaphragmatic region the milk may pour through an open cardia into the oesophageal groove. Often however the milk is denied immediate access to the stomach and it then collects in the distal end of the oesophagus which dilates to accommodate it, forming the phrenic ampulla which abuts upon the diaphragm. At other times however the gouts appear to rebound and run forwards again, often in a flattened form suggesting a pool, filling only the lower part of the dilated tube. This returning fluid may halt at the level of the heart, it may rejoin the column at the thoracic inlet or, and this is quite frequent, it may shunt to and fro several times before it eventually succeeds in finding the exit from the oesophagus unobstructed.

The amount of milk found in the thoracic oesophagus at any one time varies; in the early part of the feed large quantities may proceed from pharynx to stomach without delay in the manner suggested by Benzie & Phillipson. Later when the arrest at the thoracic inlet is more frequent it is common for small quantities to be detached from this column, held at some point in the thorax and then released to proceed through the cardia: these are followed at intervals by succeeding boluses. The reason for this occurrence is not easily understood since at other times it appears that the cardia opens readily only when considerable masses lie against it and the passage of small gouts is often delayed until they are reinforced by later increments. On the other hand, a too long column of milk may not pass through undivided but is commonly split by a constriction which appears a little in front of the ampulla: if this division occurs the distal fraction runs into the stomach while the remainder is left in the thorax. It appears doubtful that the level at which this division occurs corresponds to the diaphragmatic sphincter described by Dougherty & Meredith (1955). Certainly it does not always appear at precisely the same level.

On completion of the feed the final gout may remain for some time before the cardia suggesting that the stimulus of the pharyngeal movements prompts the opening of the lower sphincter.

It may be noted that there did not appear to be any correlation of the respiratory movements with the entry to the stomach: but as sucking is invariably accompanied by considerable activity and movement of the trunk it is impossible to be certain on this point.

A less common observation concerns the upper end of the oesophagus. It has already been remarked that this, with the adjacent part of the pharynx, appears constricted and it may be noted that, particularly in recumbent animals and during the later stages of the meal, milk may be temporarily arrested in this site. But it in no way follows that because the passage of the milk is delayed at this level it will not also be obstructed again at the junction of neck and thorax.

Each swallowing movement results in the passage of air into the oesophagus and this generally precedes the milk although some becomes mixed with this and produces a very obvious 'bubbly' appearance. Apart from these bubbles the appearance of the bolus is relatively constant. Each is usually tapered at each extremity, the constricted ends being longer in the cervical than in the thoracic region and normally its contours are not interrupted between these parts by indentations such as would be produced by peristaltic waves.

<u>Discussion</u>.

The foregoing description of the oesophageal movements is included mainly for the sake of completeness and to place the appearances on record for it is gradually becoming accepted that interpretations of oesophageal activity, and of the cardiac mechanism in particular, which are based upon radiological methods of examination may provide a superficially convincing yet wholly erroneous view of the true situation (James).

It is however interesting to compare the observations made during deglutition with the descriptions provided by Dougherty and his colleagues of the process of eructation: many of the features independently recorded for these quite different activities show close agreement. In a paper devoted to this problem Dougherty & Meredith (1955) give an account of a cinefluoroscopic study of the participation of the anterior part of the ruminoreticular sac and of the caudal part of the oesophagus. Omitting reference to the gastric movements their account may be summarised as follows: gas is discharged from the stomach following the second reticular contraction and passes through the relaxed cardia into the terminal part of the oesophagus which is dilated: the gas shadow reveals the existence of a constriction some two inches before the cardia and this they term the diaphragmatic sphincter (the expression is used to point the analogy to a similar formation described in other animals (see for example Jackson, 1922) and does not indicate the topographical relationships): repeated alternations of contraction and relaxation of the two sphincters were observed while the gas was trapped in the oesophagus: finally closure of the two sphincters was followed by the contraction of the oesophageal walls and the expulsion of the gas in a cranial direction.

A second paper (Dougherty & Habel) extended the observations to the remaining parts of the oesophagus. This established the existence of yet a third sphincter about the cranial extremity of the organ conforming in position to the extent of the cricopharyngeal muscle and the adjacent circular fibres of the oesophagus. This sphincter remained contracted while the oesophagus filled with gas: when it eventually relaxed the caudal sphincter closed and the contractions of the oesophageal walls rapidly cleared the gas from the organ. The cranial sphincter could not be overcome by the artificial increase of intraruminal pressure. They also reported irregular but pronounced 'sphincterlike' activity of the oesophagus at the thoracic inlet.

The existence of the cranial sphincter and the specially active region at the inlet which was seen to provide an obstruction to the flow of milk are thus amply established: some doubt attends the identification of the more caudal obstruction. The

American workers regard it as fixed in position and they have Helm's authority for the existence of a thickening of the circular muscle of the oesophagus at this location. The results presented here do not support this view: the constriction which sometimes appeared to divide the column of ingesta in this region had a more variable position than was assigned to the diáphragmatic sphincter but possibly it may be regarded as its functional equivalent since no evidence was obtained for the presence of a fixed muscular barrier. It may be the case that there is here a true species variation for both the Americans and Helm refer to sheep, our observations apply to the goat.

The constriction that appears on the oesophagus as it passes through the diaphragm cannot be identified with certainty but there is a strong presumption that it is caused by the crura of the diaphragm: it lies too far forward and is too extensive and pronounced to agree with one's preconceived notions of the weakly developed cardiac sphincter and this explanation moreover concurs with the appearance in the dead animal.

It is evident however that the whole region requires a more detailed study by gross and microscopic methods than it has yet received.

The mechanics of rumination have been deliberately excluded from consideration in this thesis:

an excellent account of the radiography of the oesophagus during this process is provided by Aleev (1952).

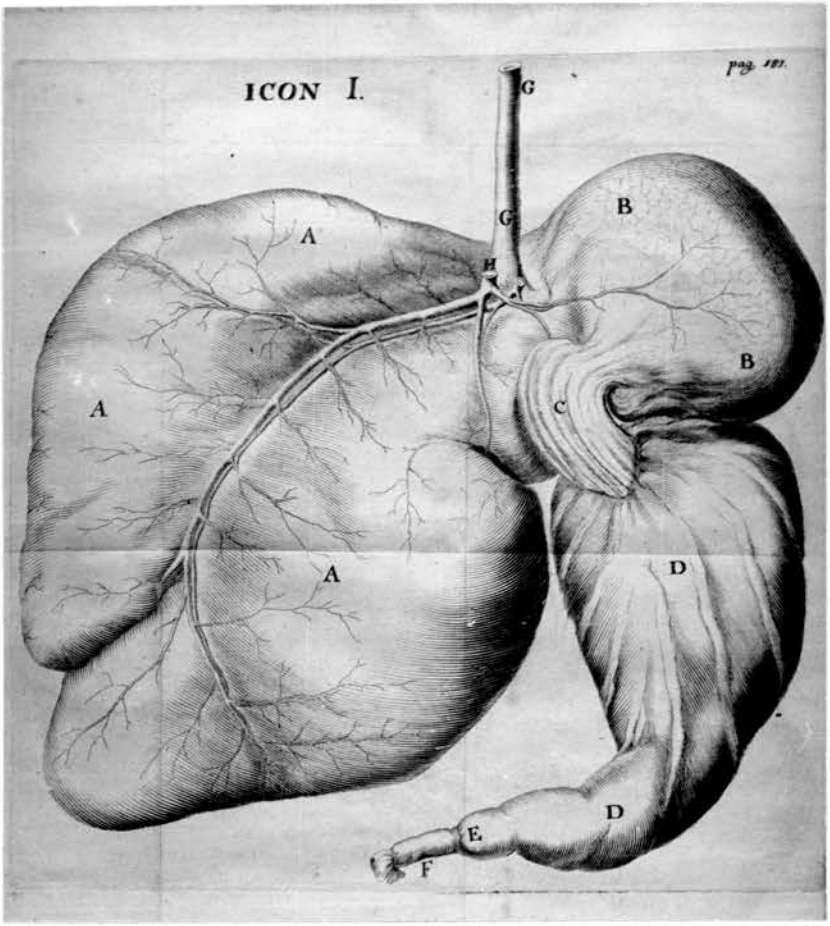


Fig. 9 Peyer's illustration of the stomach of the goat as seen from the right with the abomasum displaced ventrally.

A.	Rumen	E.	Pylorus
B.	Reticulum	F.	Duodenum
C.	Omasum	G.	Oesophagus
D.	Abomasum	H.	Gastric artery

This drawing gives as good as, or a better suggestion of the divisions of the stomach than any picture in later works.

The Rumen and Reticulum

Radiological Anatomy

General considerations.

The rumen and reticulum are best considered as a common sac for while their separation for purposes of description is usual it is artificial on both morphological and functional grounds. The junction of the two chambers is sufficiently exactly indicated by the ruminoreticular fold and by the entrance of the oesophagus (figs. 9, 10 11 & 32, plate 2).

The reticulum is situated immediately behind the diaphragm and while extending across the midline it yet lies always rather more to the left. In older animals it reaches the abdominal floor in the region about the xiphoid cartilage when it is relaxed and in these circumstances there is often to be seen a double outline of the posterior margin which indicates the moulding of the organ to fit the anterior part of the fundus and corpus abomasi (fig. 33, plate 3). Hoflund (1940) regarded this as an abnormal state and in reproducing such a film claimed it as typical of abomasal dilatation following upon pyloric stenosis. It is, on the contrary, a very common finding in normal goats. Certain radiographs, particularly of the partially contracted state, portray the outlines of the septa which divide

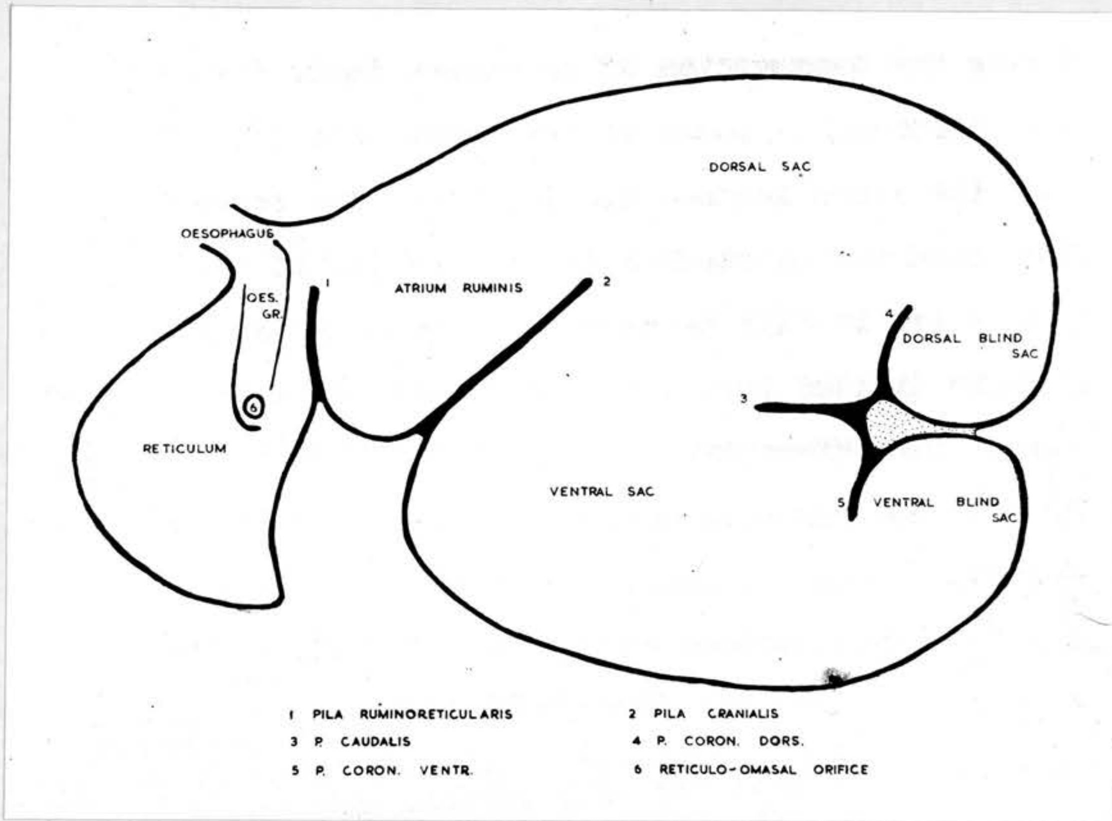


Fig. 10 Schematic representation of a generalised ruminant stomach. In the goat there is no dorsal coronary pillar while the ventral coronary pillar springs from close to the margin of the caudal pillar.

Compare with figs. 11 and 33

the internal surface into the characteristic honeycomb (fig. 12) and other films, suitably timed during the consumption of an opaque feed, demonstrate the oesophageal groove on the right wall (fig. 7).

The rumen is more complicated. Its general conformation may be studied in figures (9, 10 and 32) from which it will be seen that the organ is incompletely divided into a series of compartments by permanent infoldings of the wall which form the pillars. In life the rumen is active and the shape and proportion of each of these parts is continually altering but these changes do not greatly affect the general position of the organ since they are in large measure reciprocal and the space vacated by the contraction of one compartment is normally filled by the simultaneous relaxation and expansion of another. Despite these activities a basic or resting phase may be recognised which closely corresponds to the form generally assumed post mortem.

It is unnecessary to consider each subdivision in turn since their mutual relationships and connexions are sufficiently evident in the photographs and radiographs. One compartment however possesses particular interest: this is the anterior dorsal sac, otherwise variously known as the anterior sac, the anterior blind sac, the atrium ruminis or, by German authors, die Schleudermagen. This part is in free communication with the cavity of the retic-

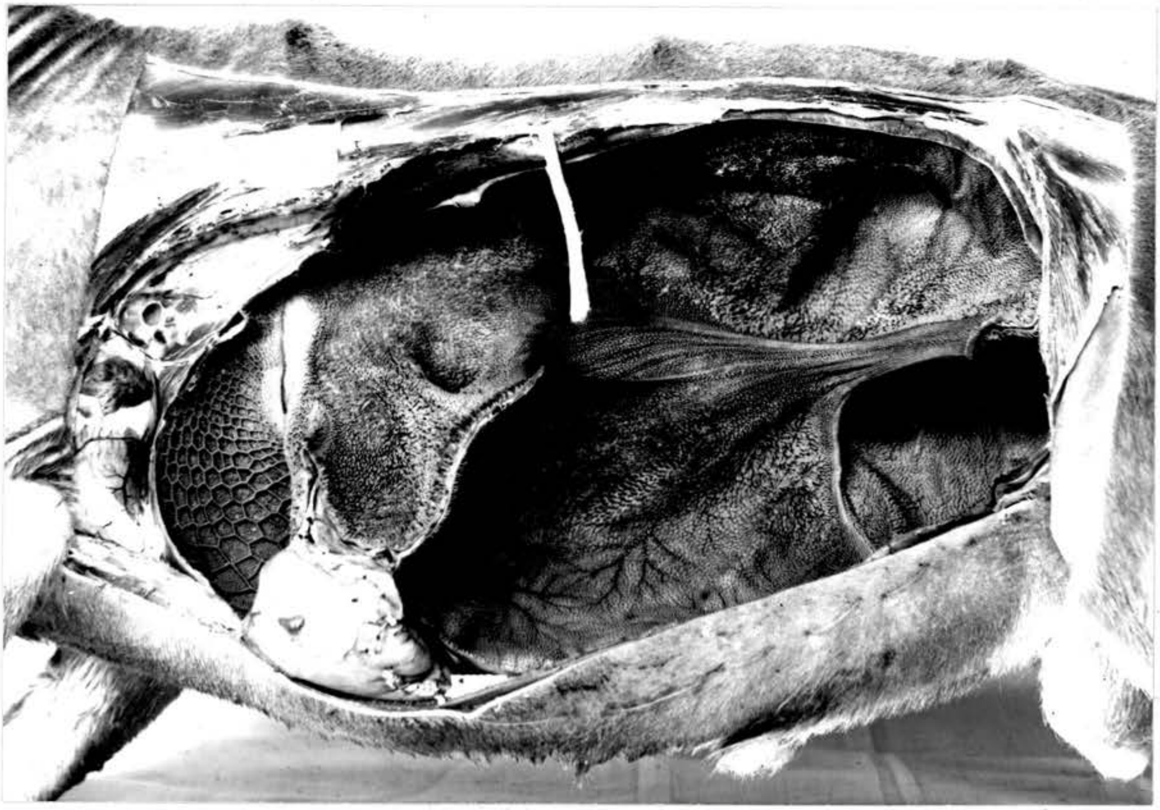


Fig. 11 The interior of the rumen and reticulum of a six month old goat - at this age the anatomy of the abdomen is virtually adult.
Note the pillars, the oesophageal groove and the nature of the mucosal linings.

ulum over the ruminoreticular fold and is limited caudally by the oblique direction of the anterior pillar. The cardia or entrance of the oesophagus occurs where the atrium ruminis joins the reticulum dorsally and it will be remarked that in neither the live nor dead state is there any evidence of a dome or funnel shaped atrium ventriculi as was once described at this location.

Certain additional details of radiological interest may be noted. The disposition of the ruminal contents may be studied in radiographs obtained in the standing position (e.g. fig. 29): in these the upper part of the organ is found occupied by gas which is bounded ventrally by fluid in which the heaping of the more solid fraction may sometimes be discerned: commonly, and especially in younger animals, the solid materials project above the fluid level in which case they interrupt the gas shadow in irregular fashion. A striking concentric arrangement of the coarser solids to which Phillipson first drew attention is sometimes visible and demonstrates the rotary movement imparted to the ingesta by the ruminal contractions (fig. 13). A further feature very evident in some plates of older kids is a stippling of the ruminal image produced by the interruption of the shadow of the contrast agent by the papillae which adorn the organ internally (fig.35).

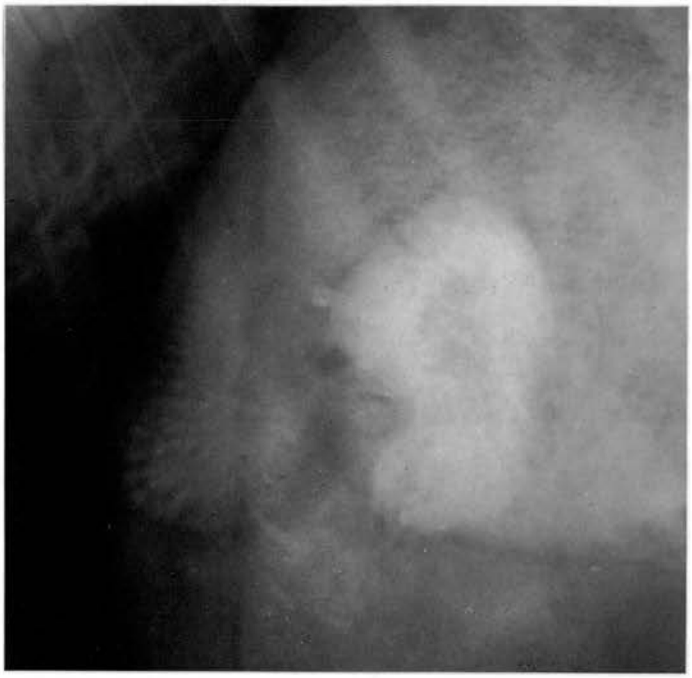


Fig. 12 A view of the semi-contracted reticulum showing marginal interruptions of the shadow produced by the walls of the 'cells'. The omasum is also shown and it will be observed that its upper part is dilated, its lower pole contracted.

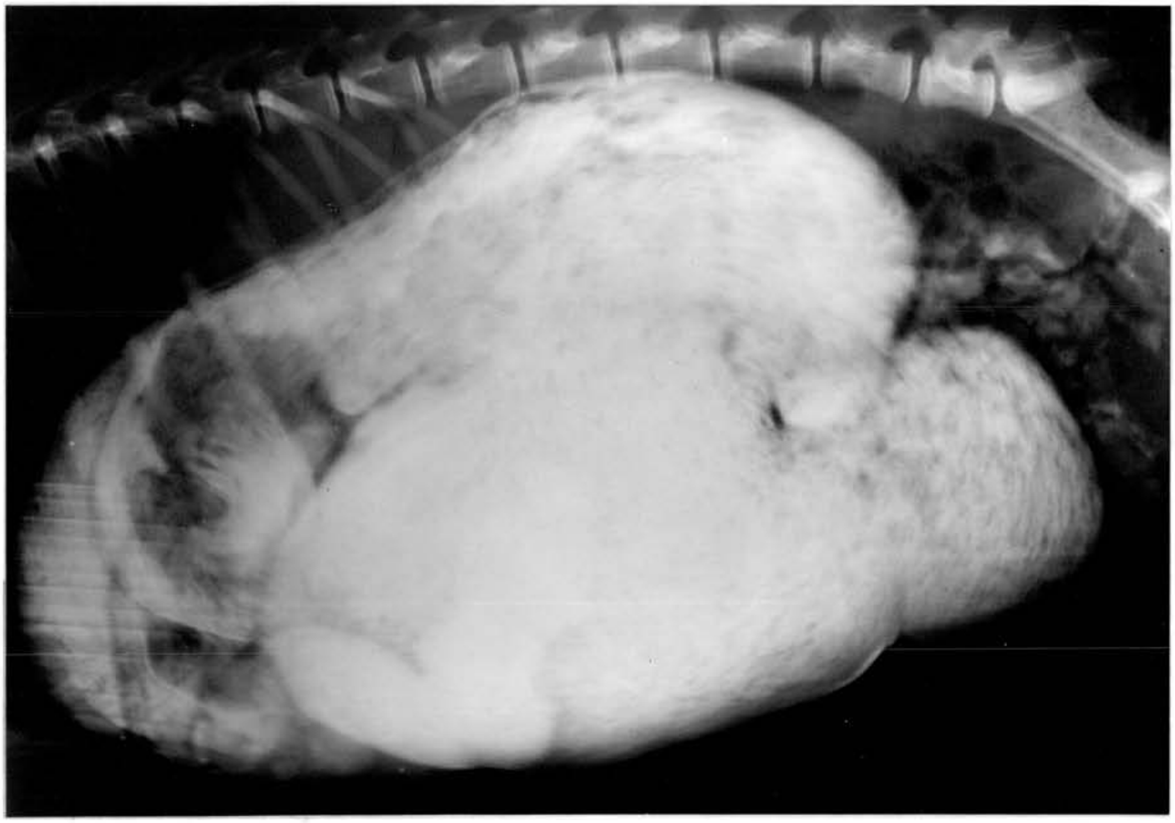


Fig. 13 This animal was aged 10 weeks. A circular arrangement of the ruminal contents may be observed. The omasum and abomasum are also visible.

The movements are discussed shortly but a preliminary comparison of several plates from the same animal will demonstrate the variations in the size of the parts and in the thickness of the pillars depending upon the degree of contraction of each (for example, frames 6, 17 & 25 of the series reproduced on Plate 2).

Postnatal development.

The changes in the rumen and reticulum that take place during the growth of the kid are very marked and as the development of the two organs runs parallel the events may be traced in the same series of radiographs. In the newborn animal neither the rumen nor the reticulum has any function to perform and these parts are not easily studied since they are by-passed by the milk meal which normally proceeds by way of the oesophageal groove and omasal sulcus directly to the abomasum. Fortunately a certain amount of air is swallowed during suckling and a part of this usually finds its way into the rumen to outline the upper part of the organ: it does not provide any clue to its ventral extent but dissection shows that the lower margin fails by some distance to reach the abdominal floor (fig. 14). Films obtained during the first two or three days of life and some time after a meal, suggest that the organ then lies entirely within the thoracic cage (fig. 15) but immediately after feeding the gas bub-

Fig. 14 Dissection of a kid aged one week. Note the size of the rumen and spleen and the relation of the left flank.

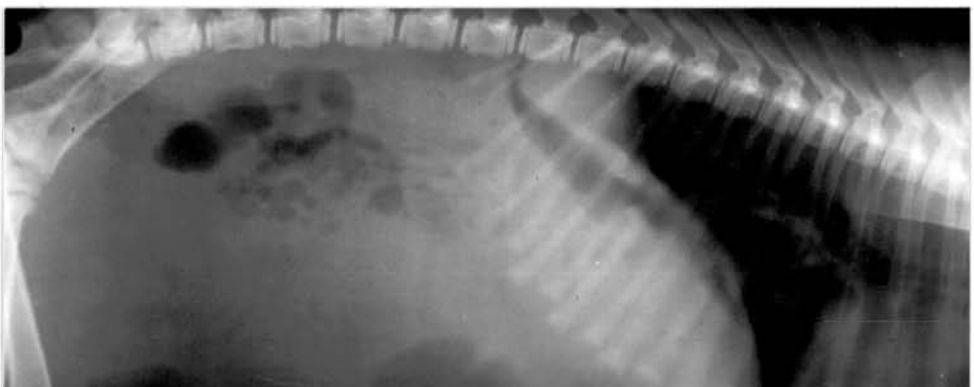


Fig. 15 Kid aged one week showing distribution of gas in fasting state.

ble is relatively large and may then extend as far back as the middle of the third lumbar vertebra: these later pictures show a forward inclination of the posterior border, indicating that the ventral part has not enlarged in the same degree (fig. 16). The appearance of the bubble suggests that it is contained entirely within the dorsal sac: presumably the ventral sac which is invisible lies below this level. Further indication of the position of the rumen may be obtained indirectly. In the dorsal view the moderately distended abomasum fails to reach the left body wall and it leaves on this side a space, amounting to a quarter of the transverse diameter of the trunk, which is occupied by the rumen and small intestine (fig. 50). The full abomasum however attains an extensive parietal contact on the left side and it then displaces the rumen dorsally and the small intestine caudally. This arrangement is shown in the dissected specimen of a week old kid (fig. 14). The reticulum is even more difficult to study in the very young for the persistence of a bubble in this chamber is less frequently demonstrated since the gas, lying ventral to the cardia, more readily escapes.

Little change is noted during the succeeding ten days or so but once this period has elapsed there is a relatively rapid increase in size associated with the interest the kid begins to show in

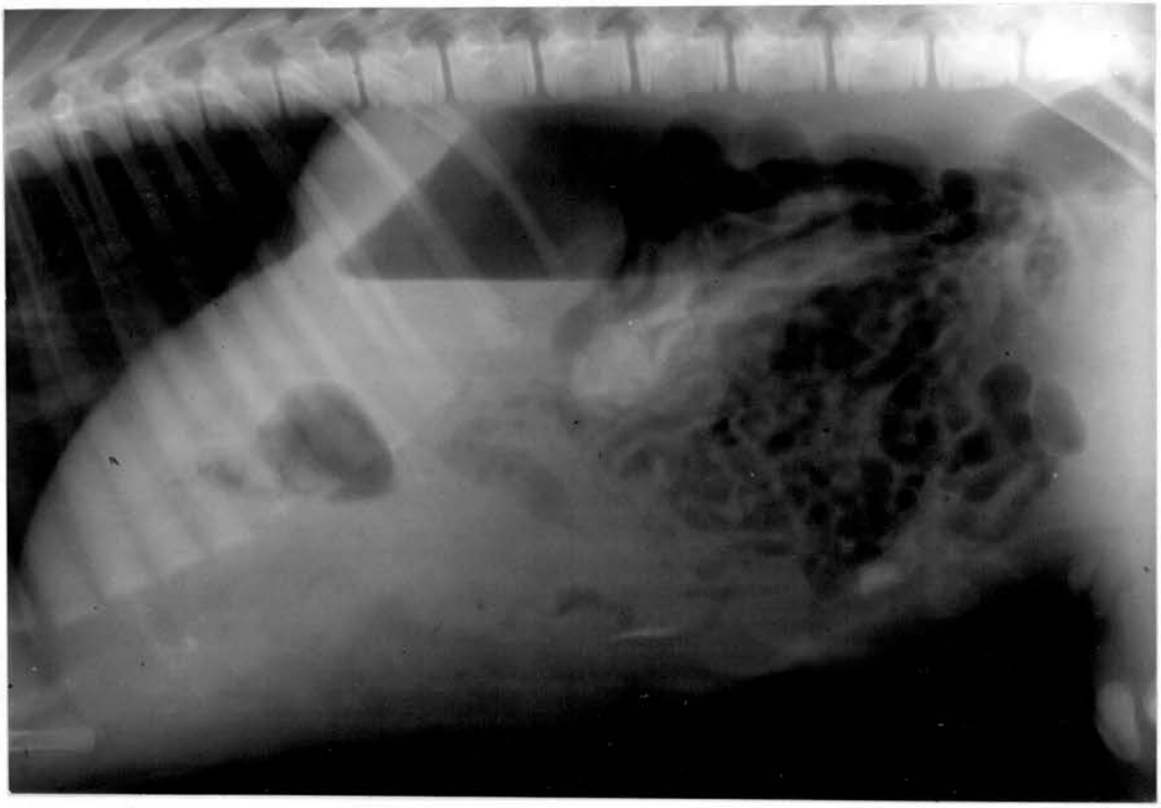
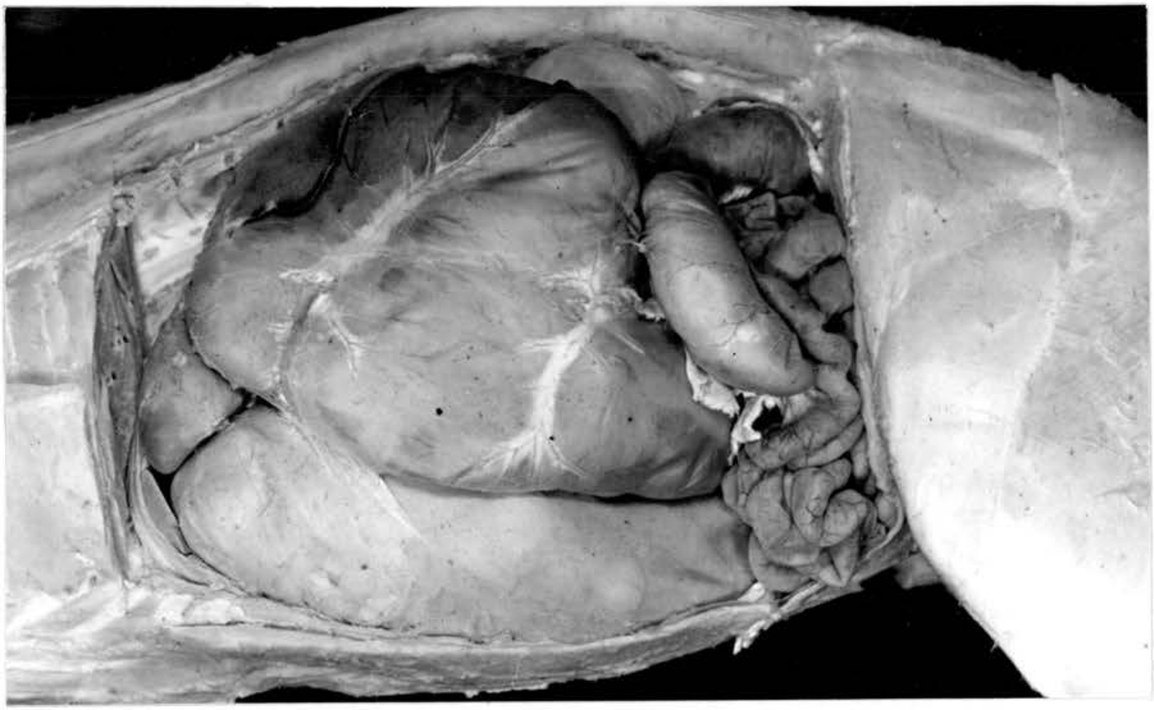
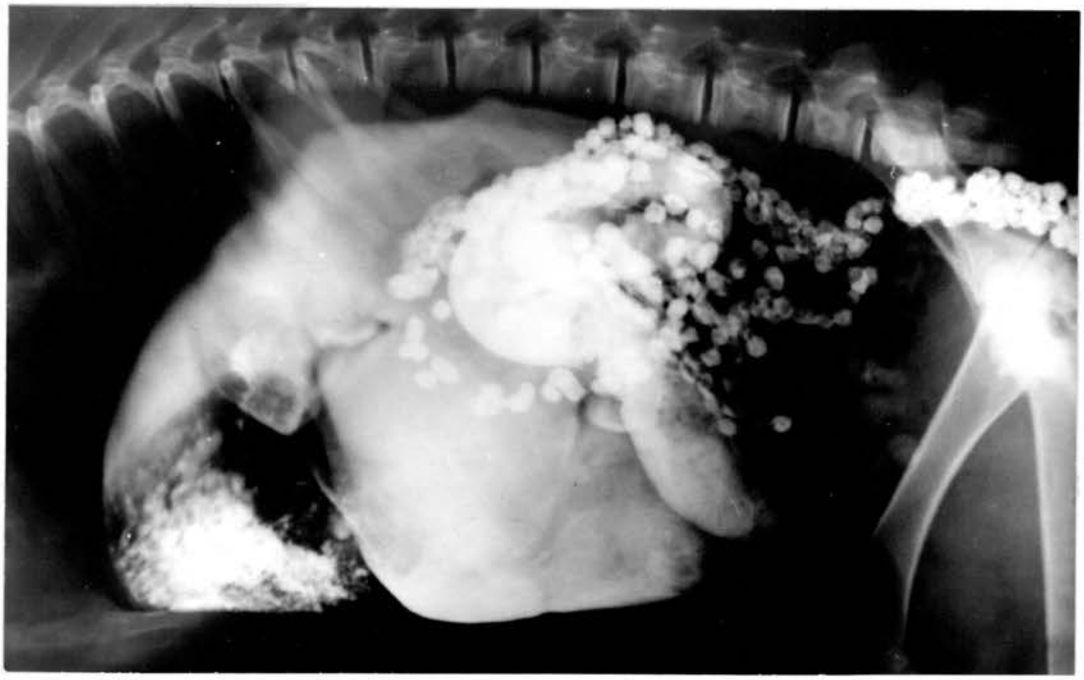


Fig.16 The distribution of gas in the abdomen of a subject aged one week immediately after bottle-feeding with plain milk. The large gas shadow in the rumen is very evident and the straight lower edge indicates that it lies above a fluid level. The smaller shadow below and in front of this is produced by the air in the abomasum. The other very numerous collections of gas lie in the small and large intestine: the rectum is seen entering the pelvis and the shadow cranial to this is probably the descending colon.

solid food and at three weeks the rumen which already shows irregular activity is surprisingly large. The general appearance of the organ at this age is shown in figs. 17 and 18. In the latter figure a quantity of contrast material lies within the rumen and in these circumstances it occupies a considererable part of the abodomen: it extends caudally to the level of the fifth lumbar vertebra and ventrally onto the abdominal floor although in this case over a restricted area only: the upper part is related to the roof of the abdomen except for a small depression in the anterior part of its surface, which lodges the spleen. The dorsal view of the same animal showed that the rumen still lies entirely within the left half of the abodmen although posteriorly it approaches but does not yet reach the midline. In most plates obtained at this age the ventral blind sac appears to reach further caudally than the dorsal but since these parts are now quite active the relationship is not permanent. The variation that may exist in the same animal is very strikingly shown by a comparison of two figures in Czepa and Stigler's second communication. In one (their fig. 15) the stomach is shown after a feed which has reached all four chambers: in the other (their fig. 17) the same kid is shown two days later with the rumen filled by gastric sound and now apparently three or four times its former size.





Figures 17 and 18 show the postmortem and radiographic appearance of the viscera in the same subject, aged 20 days. The radiograph shows two meals: the first lies in the large bowel and was administered 48 hours previously. The second outlines all four chambers of the stomach.

Usually at this age (three weeks) there is a considerable enlargement of the reticulum which when expanded extends far ventrally and while still not in contact with the abdominal floor yet lying at no great distance from it. It does not as yet debar the abomasum from contact with the diaphragm.

At four weeks the rumen usually has an extensive contact with the abdominal floor and it is conspicuously enlarged in its vertical diameter (fig. 19). The animal is now, of course, consuming much solid foodstuff but the taste for this is not uniform and while further progress is rapid considerable individual variations appear in the conformation of the stomach which very likely have as their cause the varying readiness with which the animals eat the fodder. Figures 20 and 21 are of an animal aged between five and six weeks in which ruminal and reticular development are particularly advanced. The rumen is displayed occupying the entire left body wall from the ninth intercostal space to within a short distance of the pelvic inlet, leaving only a small space opposite the tenth to twelfth ribs for the spleen and a triangular gap behind the reticulum for the abomasal fundus. The rumen extends considerably across the midline posteriorly where the ventral sac lies relatively close to the right flank. The ventral blind sac is again the most posterior part of the organ and rests upon the

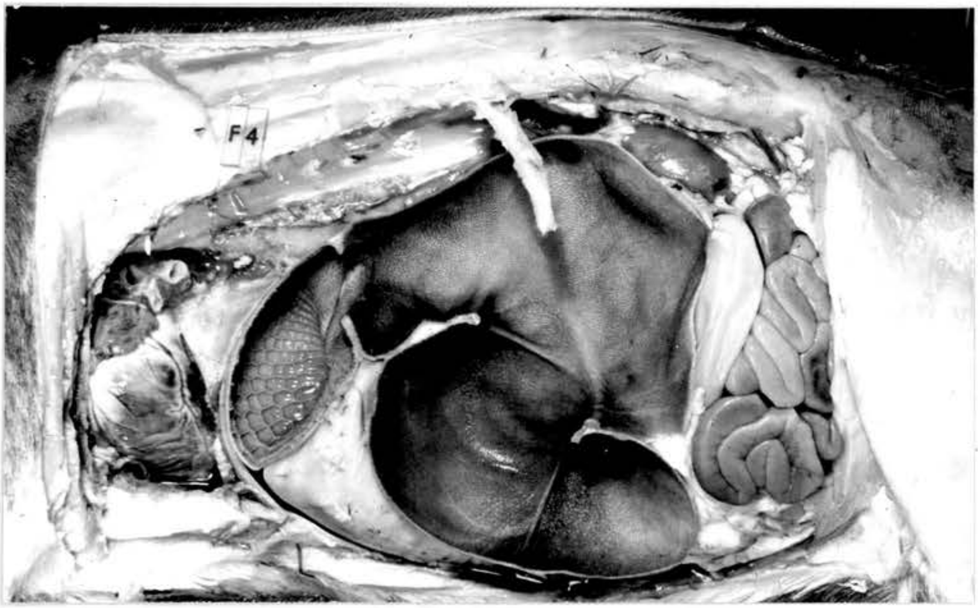


Fig. 19 Dissection of subject aged four weeks.
It will be observed that the rumen has an extensive contact with the abdominal floor but does not yet occupy the entire left flank. The caecum lies behind the rumen, and behind this again are festoons of small intestine. The left kidney has not yet migrated from its original position.

abdominal floor: the abomasum intervenes in front of this. In both views the anterior dorsal sac (atrium ruminis) forms a relatively constricted part joining the reticulum and apparently this region of the rumen develops more slowly than the rest. The reticulum also extends ventrally to the sternum and laterally well across the midline - an expansion which has an important but obvious bearing upon the topography of the abomasum.

A more typical appearance at the age of six weeks is provided by figure 22 which makes an interesting comparison with a similar earlier view (fig. 18). Here the rumen is of stockier form and the gap between it and the reticulum is of more normal proportions: caudally it lies about one vertebra in front of the sacral promontory and although it is in full contact with the abdominal floor the dorsal view discloses that it does not extend much further to the right than the border of the vertebral bodies. At this age the organ exhibits most of the features that characterise the adult rumen and although its size, both absolute and relative to the abomasum and abdominal cavity, continues to increase the changes are now more gradual and less obvious: accordingly it will be permissible to lengthen the intervals between the stages selected for description. Compare, however, figures 23-29.

Figures 20 & 21 The rumen and reticulum in a kid aged $5\frac{1}{2}$ weeks. The organs are particularly well developed in this animal. Note the small size of the atrium ruminis.

At twelve weeks the rumen is approaching its adult proportions and it now extends very much more across the midline (fig. 28). As a rule the ventral sac is separated from the right flank by a relatively narrow band of small intestine while even the dorsal compartment passes the border of the spine, particularly in the anterior and middle parts of the abdomen. At five months (fig. 29) the rumen has reached and perhaps passed the plane of the lumbosacral junction and frequently it excludes the small intestine from the posterior part of the abdomen except where the gut lies against the right flank: the space available to the abomasum within the left half of the abdomen is thus very restricted. It is however important to note that quite apart from the functional changes there is still a certain measure of individual variability and no single description or illustration can define the appearance in every animal.

The films of the 14 month goat show the final form assumed by the rumen (fig. 30a, b). It is difficult to assess the proportion of the abdominal cavity occupied by this organ but obviously it entirely dominates the abdominal relationships and not only substantially fills the left half of the abdomen but, especially in its ventral part, extends far into the right side.

Fig.22 General view at 6 weeks. The rumen, reticulum, omasum and large bowel are prominent. The abomasum still preserves some contact with the diaphragm below the reticulum but it is poorly shown. A collection of the contrast agent lies in this organ.

The omasum is appreciably enlarged. The caecum and proximal colon extend far ventrally and the former apparently is related at its apex to the abdominal floor.

Fig.23 General view at 9 weeks.
There is further development of the omasum and the abomasum still extends far caudally. The large bowel is now restricted to a more dorsal position except for the final centrifugal coil which ranges widely. Immediately above the caudal extremity of the abomasum may be recognised the first centripetal coil of the spiral colon with its tonic constrictions.

Fig.22 Legend on reverse.

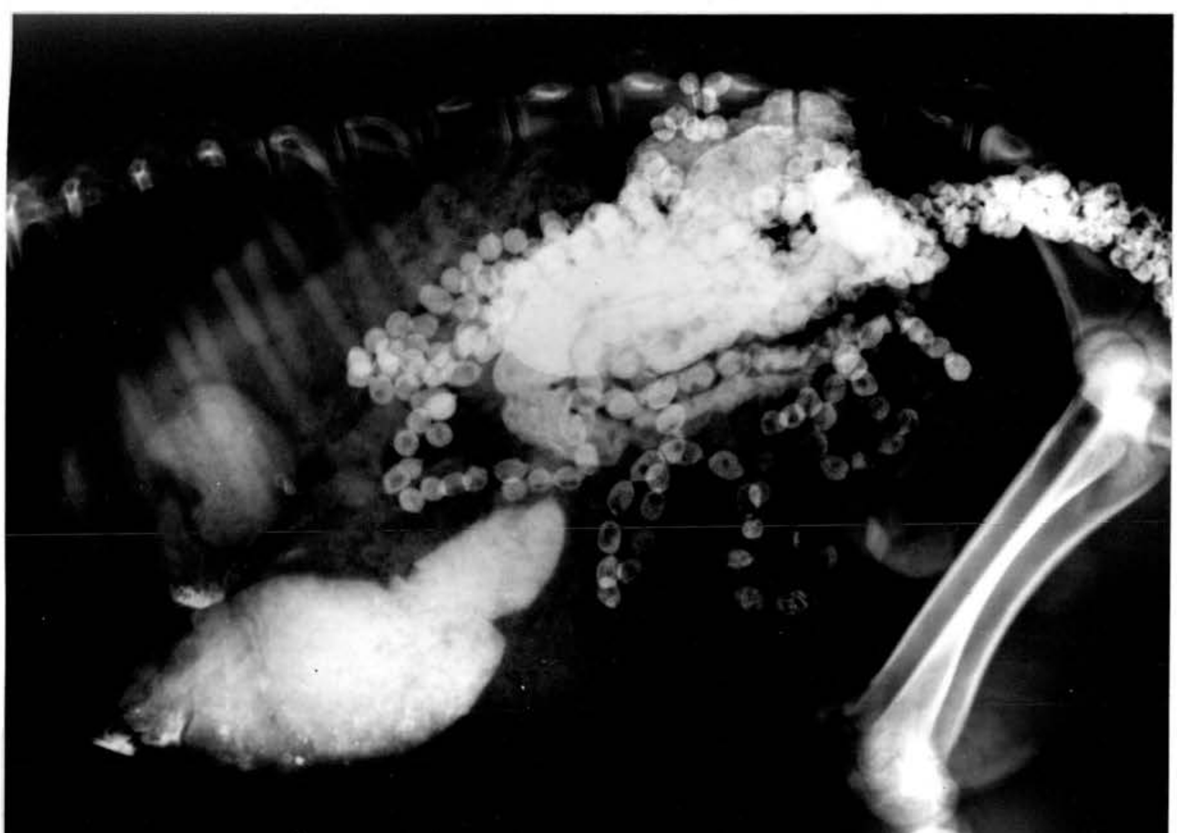


Fig.23 Legend on reverse.

The late development of the reticulum may be even more simply summarized. It continues to increase in size and to push across to the right where it comes into contact with and is flattened by the liver: behind this it is related to the omasum (fig. 27). At the same time it enlarges into the space previously occupied by the abomasum which is thrust backwards and to the right and as the abdomen becomes increasingly protuberant the reticulum dips below the level of the xiphoid process of the sternum (fig. 26). Little alteration in its configuration or relative size can be determined after the animal reaches the age of four or five months.

Ruminoreticular motility.

Previous literature.

The movements of the ruminoreticular sac are not of a uniform nature. The basic pattern of activity is adapted to securing a continuous circulation and mixing of the ingesta but superimposed upon this are the extra and irregular contractions necessary for the processes of eructation and rumination: in addition small localised contractions are also observed. In this study observations upon the events associated with the eructation of gas and with the regurgitation of the ingesta were limited in their scope and were insufficiently extensive to

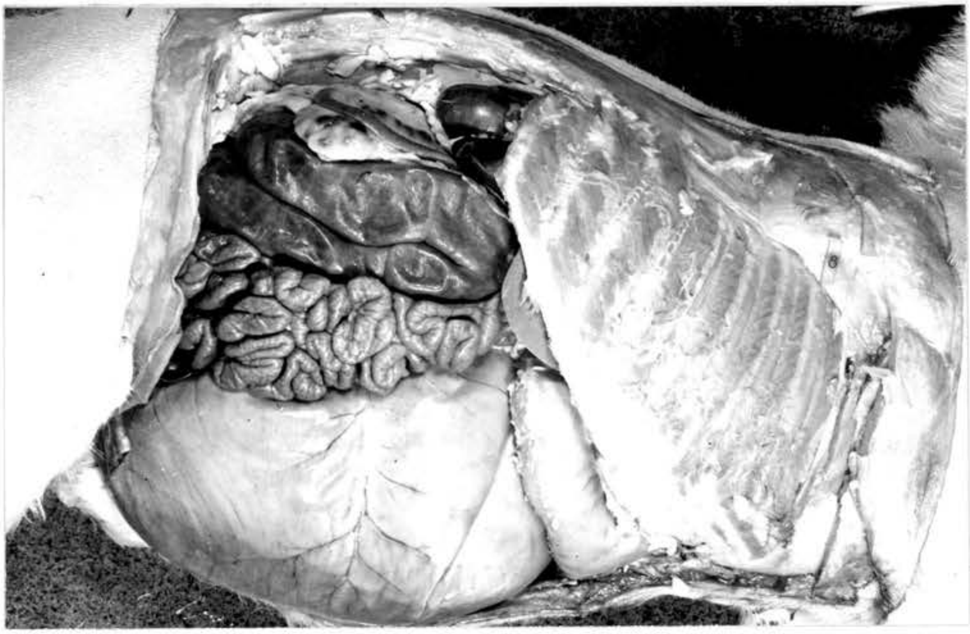
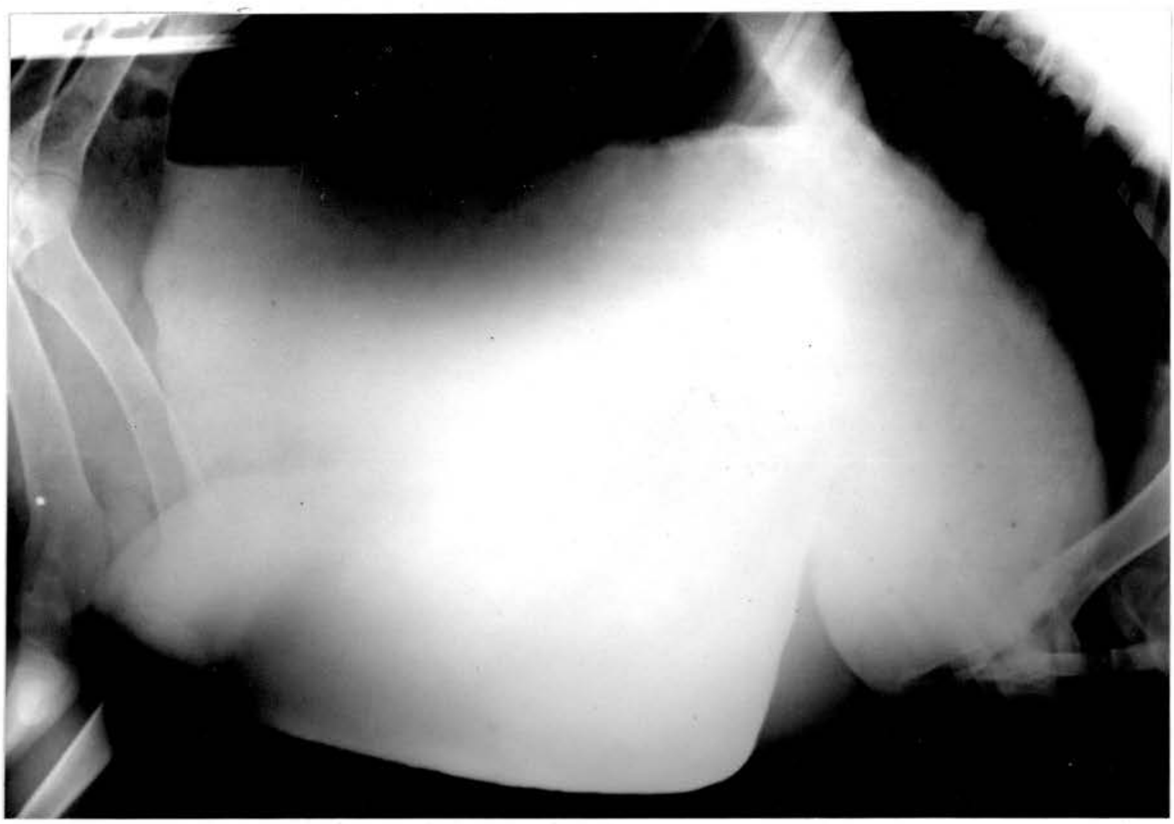


Fig.24 Eight week old specimen. The rumen now figures prominently on the right side and the intestines are dorsally displaced. Note also the tubular form of the pars pylorica just behind the costal arch. The liver appears at a higher level than in the previous figure - much individual variation affects this and the other topographical details.

confirm or controvert previous descriptions: they are therefore omitted from consideration and reference must be made to the papers of Aleev (1952), Weiss (1953), Dougherty & Meredith (1955) and the various publications of Stigler (1931, 1933 & 1948) for a discussion of these aspects.

Before proceeding to the examination of the mass contractions of the rumen and reticulum it is necessary to refer at slightly greater length to the localised contractions already mentioned. These appear to be peristaltic in nature and they take the form of static or slow moving indentations, generally on the ventral and cranial walls of the rumen. Czepa and Stigler (1926) described and illustrated them in a form suggesting a rather more vigorous type of activity than was apparent to most later workers. All who have reported their occurrence agree that they were absent on the reticulum. Duncan (1951) observed that they have been ignored in many recent papers and suggested that while they may possess only a very minor intrinsic importance, they are possibly of greater significance as a source of error in the interpretation of experimental results, particularly those obtained with isolated portions of stomach wall. She regarded them as characteristic of the spontaneous contractions of smooth muscle.



Figs.25 & 26 Dissection and Radiograph of subject aged 8 weeks. The rumen now occupies virtually the entire left half of the abdomen.

The ruminoreticular cycle has been described by numerous investigators who have employed a variety of techniques and animals of different species and age. It is hardly surprising in these circumstances t hat their accounts conflict in detail. The work of Wester (1926: the common practice of citing this paper is followed although it was in fact preceded by several years by a Dutch version) is generaly regarded as initiating the modern study of the subject. This author used cattle in which he produced rumen fistulae through which he observed and recorded the pressure changes in the ruminal compartments. He described a double contraction of the reticulum followed by the successive contraction of the rumen sacs and he regarded the whole cycle as being due to the spread of peristaltic waves from the region of the cardia, the waves extending forwards over the reticulum and backwards over the rumen and eventually reaching the omasum. This interpretation of these events is no longer acceptable but his theory had the great merit of focussing attention upon the co-ordination of the activities of the stomachs and of those of the rumen and reticulum in particular. The experiments of Schalk and Amadon (1928) were conducted upon very similar lines and their observations and interpretations agreed in the main with those of Wester: they described

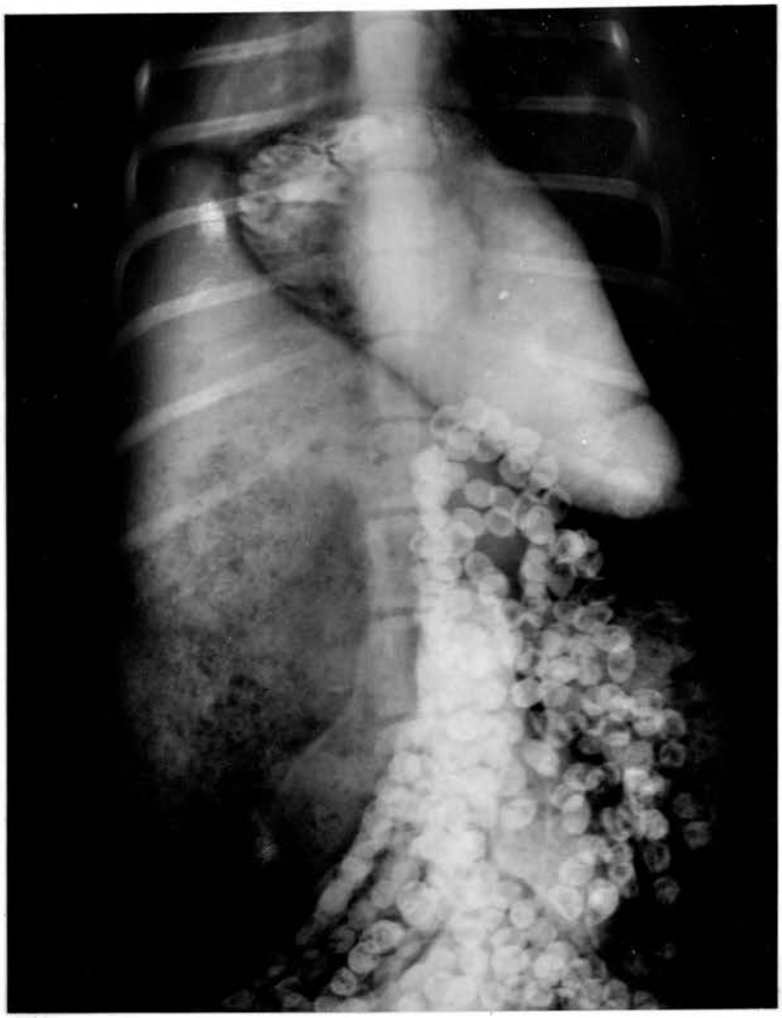


Fig.27 Ventral view showing general disposition of gastric chambers and large intestine at eight weeks. The omasum still overlies the spine but shows a bias to the right which is often more pronounced by this time. The abomasum no longer contacts the left body wall.

an additional wave of contraction which was confined to the rumen and like its predecessor involved first the dorsal and then the ventral sac.

The first description based upon a radiological study was presented by Czepa & Stigler (1926) who used goats for their experiments. In place of a double contraction of the reticulum they describe a two stage contraction with an incomplete relaxation of the organ between the stages. They observed a reciprocal relationship between the contractions of the reticulum and atrium ruminis but were otherwise unable to correlate reticular and ruminal activity: the main movement of the rumen was an alternate contraction of the dorsal and ventral sacs. They were emphatic in regarding the main contractions as being total in nature and thus rejected Wester's peristaltic theory. Their later communication (1929) described the contractions at greater length, though hardly with greater precision, and they there noted independent activity of the blind sacs. They persisted in denying a co-ordination of the general ruminal contractions with those of the reticulum in the adult animal but remarked that in the young kid, before the development of the reticulo-atrial cycle, there was an alternation of the movements of the two organs which could be regarded as functioning as single units. They were therefore

Fig. 28 General view at 12 weeks.
The same parts are shown as in the previous film. It will be noted that the omasum is now considerably grown.

Fig. 29 General view at 5 months.
It is now difficult to demonstrate the stomach. The abomasum is dorsally elongated and a stream of contrast material is seen descending through the supernatant fluid.

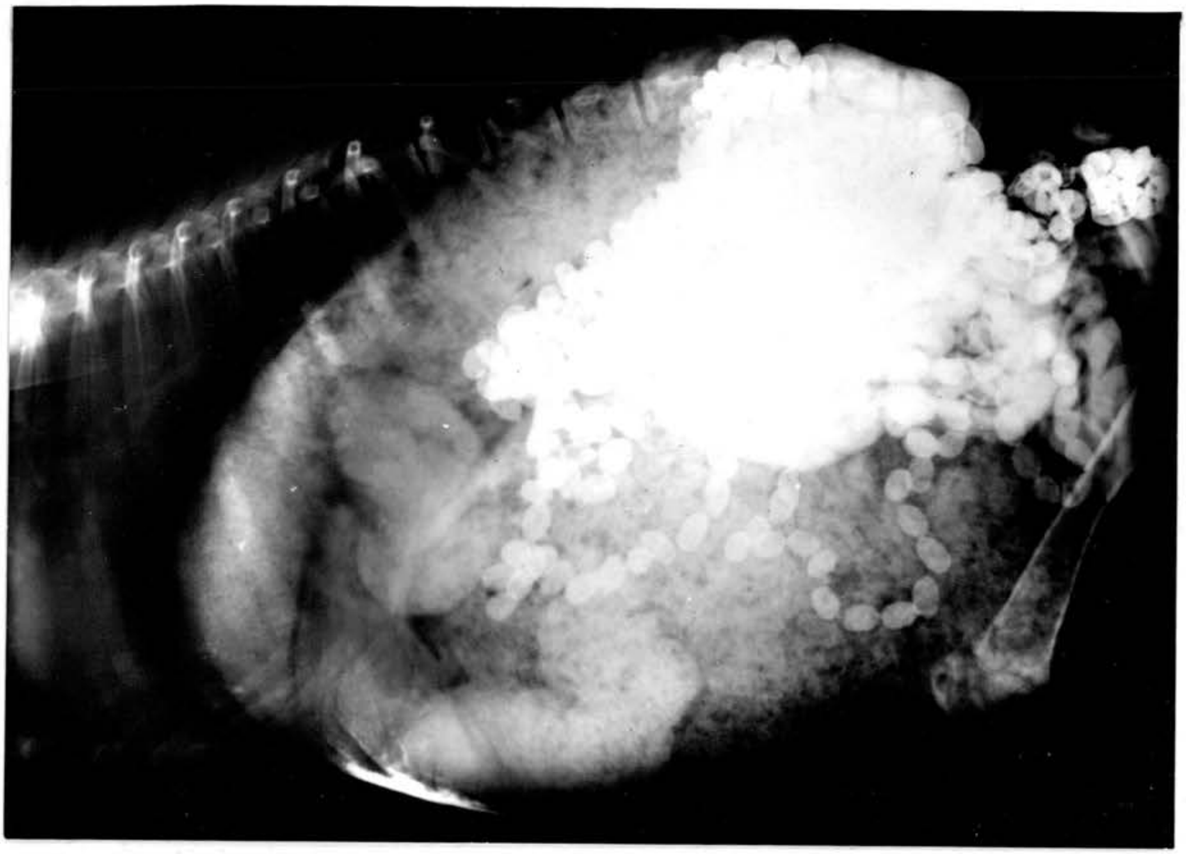


Fig.28 Legend on reverse.

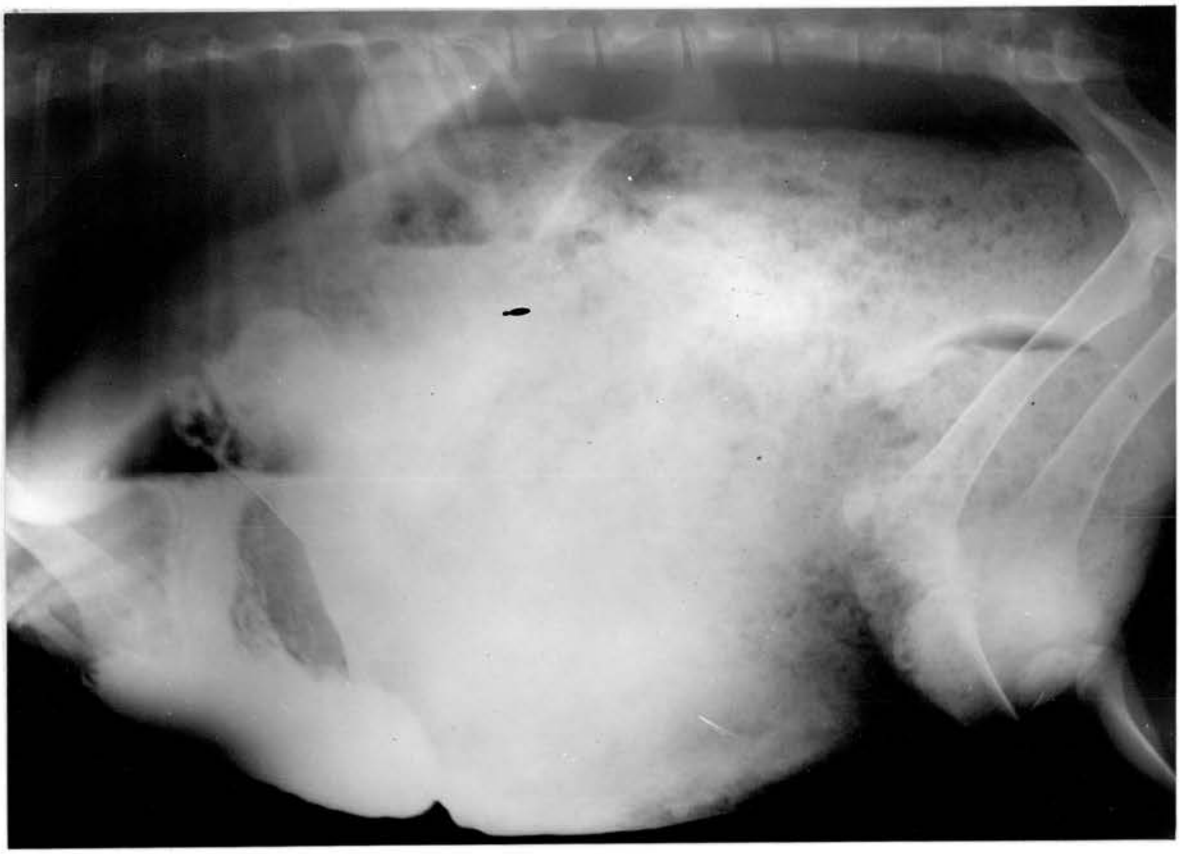


Fig.29 Legend on reverse.

aware of the existence of changes in the rumino-reticular cycle associated with age.

Magee's account (1932) of fluoroscopic observations in the same species next appeared. His description is not easily followed but he appears to have described a cycle of contractions involving the dorsal, ventral and ventral blind sac in that order. (He used the term caudal sac: Phillipson believes he meant by this the dorsal or the ventral blind sac, according to the previous state of each, but the interpretation presented here seems to fit his description better). Trautmann (1932) also studied the stomach of the kid by this method and by the use of an abdominal window. He confirmed the total nature of the main contractions but drew attention to additional peristaltic waves which carry the ingesta caudally. The cycle of events appeared to be very different in the kid and the adult: in the former the reticular contractions were more frequent and the predominating activity of the rumen was a total contraction of the blind sacs, alternating with each other and apparently of much more importance than the activities of the main compartments. The rumen cycle was repeated and followed by a pause before the next reticular contraction.

Krzywanek & Quast (1937) reverted to the method of pressure recording and they registered

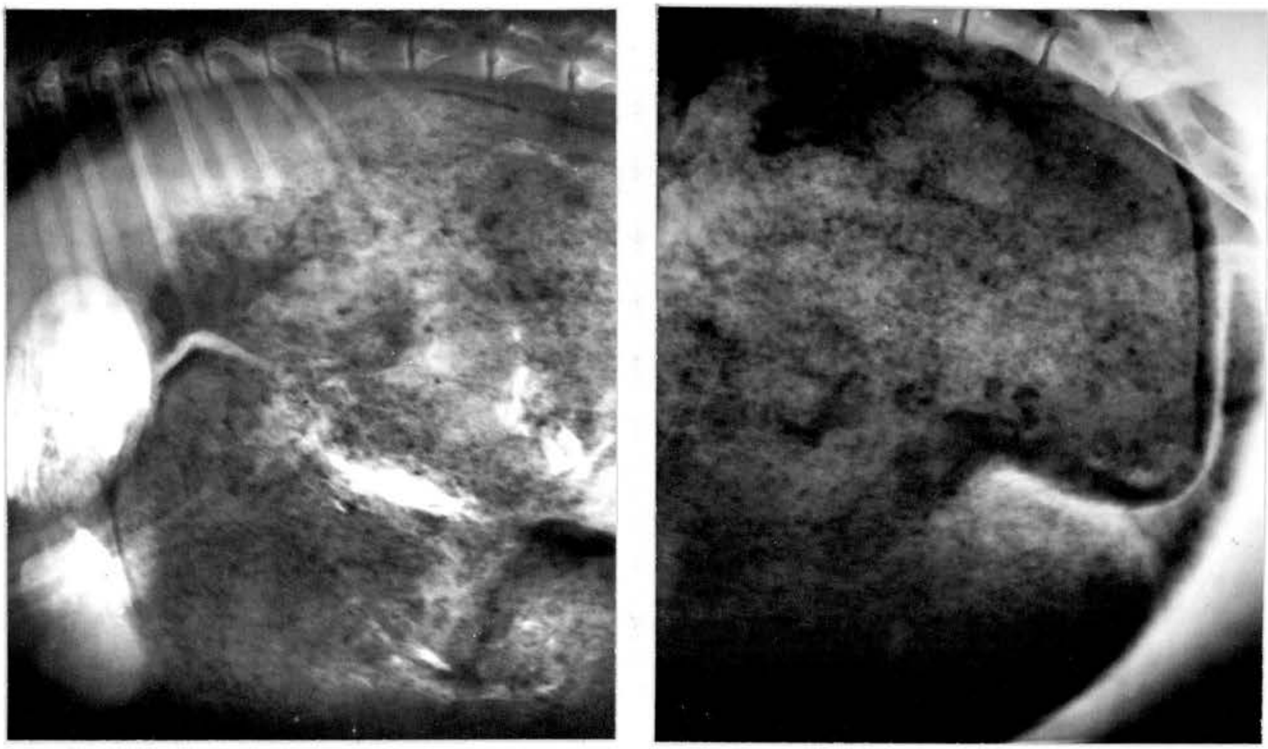


Fig.30 a & b. These two films show the extent of the rumen in an adult animal. Each represents the field of a large cassette and the views were obtained in close succession. There is a certain amount of overlapping and central displacement of the caudal section.

In the cranial film the omasum is very conspicuous and the pyloric part of the abomasum is seen at the same transverse level. A streak passes back from the omasum representing the first part of the ventral limb of the horizontal loop of duodenum.

In the caudal film the left kidney is seen lying below the last three lumber vertebrae.

three main pressure waves separated by short intervals, the cycle recurring after a longer pause. They appeared to be rather doubtful of the exact interpretation of this record. The most detailed and precise description of the cycle was presented by Phillipson (1939) who studied the movements in lambs by fluoroscopy and in older sheep by pressure tracings. In the adult animal he confirmed the two stage reticular cycle and found this linked with a two or four stage ruminal cycle, there being considerable variation in the sequence in each animal. His fluoroscopic observations were in the main confirmatory and he expanded Trautmann's observations on the development of the characteristic motility in the young animal. Like others who have used radiographic techniques he rejected Wester's theory which he believed stretched the definition of peristalsis beyond its customary limits.

In a more recent study Brunaud & Dussardier (1953a) returned to the use of fistulae and pressure recording in cattle. Their results added little to previous knowledge: they noted that the contractions of the rumen and reticulum did not follow immediately upon each other and they attached considerable importance to the existence of a refractory period.

Numerous other papers dealing with this subject are omitted from consideration since they either contribute little additional information or because they use methods whose validity is doubtful. Included in the last category are the studies on laparotomised sheep by Mangold & Klein (1927) and Duke & Sampson (1937), and the investigation of Toman (1928) who used the string galvanometer to detect the activity of the rumen muscle.

Benzie & Phillipson (1957) have recently secured cine fluoroscopic films of the movements which should be most valuable: unfortunately the extracts so far published have been badly reproduced and do not allow detailed study.

Observations.

In presenting our own observations it will be simplest to commence with a description of the ruminoreticular activities of kids aged about ten weeks. At this age the animals are subsisting largely, though not exclusively, upon solid foodstuffs and some weeks have elapsed since milk formed a major part of their diet. It is probably safe to conclude that the adult pattern of behaviour is established and that no important changes in activity will now take place: certainly none have been recognised, although the increasing size of the abdomen makes examination difficult and serial work quite impossible in animals older than 14 or 16 weeks.

Very little fluoroscopic experience was necessary before the difficulties of recording these events became evident. It is almost impossible to scan all parts of the screen at once and when different happenings are occurring at the same time it is difficult to carry the sequence in the mind, or to dictate a description as it occurs. It was decided therefore to record the changes upon serial exposures: many short runs, particularly of the reticular contraction, were obtained but efforts to secure a full record upon a larger series of films were only partially successful. The most satisfactory series is reproduced as fig. 32, plate 2: This was planned to commence shortly before one reticular contraction and to extend over two cycles of activity of this organ but unfortunately the reticular rhythm changed at the crucial time so that the events cannot be clearly related to these landmarks. A second effort was even less successful and further attempts at these rather ambitious series were precluded by the expense, the radiation hazard and the fortuitous results so far obtained. A detailed analysis of the more informative run is presented in the appendix. A cine fluoroscopic sequence illustrating reticular contraction is shownin figure 33, plate 3. See also figure 34, plate 4.

Although relatively unsuccessful these series confirmed the view formed during fluoroscopy that the cycle is far more complicated and less regular than most descriptions allow and some importance is attached to the objective confirmation of this opinion. It is in fact impossible to describe the cycle in detail since there is no standard sequence that is universally followed: the following account is a composite one and is based upon many screening sessions and upon the evidence of the serial films.

Contraction of the reticulum is not heralded by any detectable sign: the relaxed organ rests upon the abdominal floor in the xiphoid region and then briskly contracts to perhaps one quarter of its former size. It maintains this state for a moment and then enlarges slightly before completing the movement by contracting almost to the point of disappearance, discharging its content into the anterior part of the rumen. The whole movement takes perhaps three seconds. The organ then relaxes and refills from the atrium ruminis: when it regains its former volume it remains fixed in outline for ten or twenty or even more seconds and then slowly increases to a considerably larger size. Full relaxation persists for only a few seconds before the reticulum returns to its resting shape which now persists until the onset of the next systole. Considerable variations occur: the degree of slackening or expansion between the two stages of contraction is especially inconstant and a double (as in the ox) rather than a two stage contraction may be a more accurate description on some occasions: much more rarely the contraction is single and without interruption though this has been noted but twice. (It is possible that frames 5-7 of figure 32 show this event). Occasional very rapid and incomplete additional contractions occur and minor and irregular waves of fuller relaxation are not uncommon. The most striking variation is however in the interval between successive systoles: these intervals have been timed on very many occasions, often in order to determine when to expose serial runs of film and the indifferent results that have been obtained have already been remarked and indicate how little constancy there is. Even in the one animal there is little standardisation: there are periods when the rhythm is remarkably regular and accurate even to a second and then without warning the sequence becomes quite disordered. Not infrequently there is an alternation of long and short cycles but more often than not the sequence is irregular and the recurrence of the reticular systole capricious. A few examples will make the point with greater force:

Kid 53/1 aged 15 weeks. Barium sulphate administered by tube at 9.15 a.m. and food withheld thereafter. The figures indicate the intervals (in seconds) between successive contractions.

10.15 a.m. 55-55-55-55-54-55
11.30 a.m. 45-63-45-65-48-63
12.30 p.m. 45-60-50-55-80-55

As it happens each of these sequence averages almost exactly 55 seconds but often no such regularity is apparent and the agreement in this case is probably coincidental.

The twin of this animal was similarly examined on the following day when it showed a cycle varying from 25 - 75 seconds, with no detectable order or symmetry in the intervals. Even greater variation is common - in one example the interval varied from 55 to 165 seconds, generally falling within the range 75-105 during a period of observation that lasted only fifteen minutes. The figures quoted relate to animals studied while deprived of access to food but not ruminating. Rumination and feeding both appear to quicken the rate though in an unpredictable fashion.

Turning now to the movements of the rumen it is appropriate to commence with mention of the relaxation of the anterior dorsal sac that invariably coincides with the second stage of reticular systole. As this chamber enlarges it displaces the adjacent part of the abomasum forwards and because of this the movement is detectable even in those animals in which the forechambers are without an opaque content. There is a simultaneous extension of the obliquely placed anterior pillar which helps to wall off the cavity of the atrium from that of the rest of the rumen and most of the reticular contents are thus deposited in this part. Contraction of the anterior dorsal sac follows as the reticulum relaxes and it precedes by a short interval the contraction of the dorsal sac. This latter change is accompanied by a relaxation of the ventral sac and of the caudal appendage of this, and it is most easily recognised by the dorsal displacement of the cranial and caudal pillars. The development and persistence of these changes takes ten or fifteen seconds and the movement is then reversed, the ventral sac contracting, the dorsal one expanding. Contraction of the ventral part of the rumen appears to begin in the blind sac and thence spread forward to the major ventral sac. After a roughly similar period the dorsal part again contracts, though less markedly, and on relaxation of the ventral part the rumen adopts an intermediate or 'resting' form similar to that familiar in the dissection room.

Thus far the cycle is fairly regular and agrees with the usual descriptions: according to these there should now follow either a pause of considerable duration persisting until the next reticular movement or else a second cycle of ruminal contractions and then this suspension of activity. These sequences are in fact often encountered but more usually there is a spell of activity which is less easily characterised and which while involving contractions of the main ruminal sacs, is further complicated by independent activity of the blind sacs. These changes are often less marked than those which have gone before and the movements towards enlargement or constriction may be reversed before they have proceeded far. Commonly the most active part is the ventral blind sac which often appears to have a rhythm independent of the remainder of the stomach and involving recurrent systole at ten or fifteen second intervals: sometimes this is followed by contractions of the part that lies in front and at other times it is without this sequel. Separate movements of the dorsal sac and of its diverticulum are much less frequent and when they occur are also less forceful: if a contraction of this part is rather more pronounced than usual it may be followed by a similar more intensive change in the ventral sac and together this may be interpreted as a second major cycle - but such an occurrence is by no means constant. It

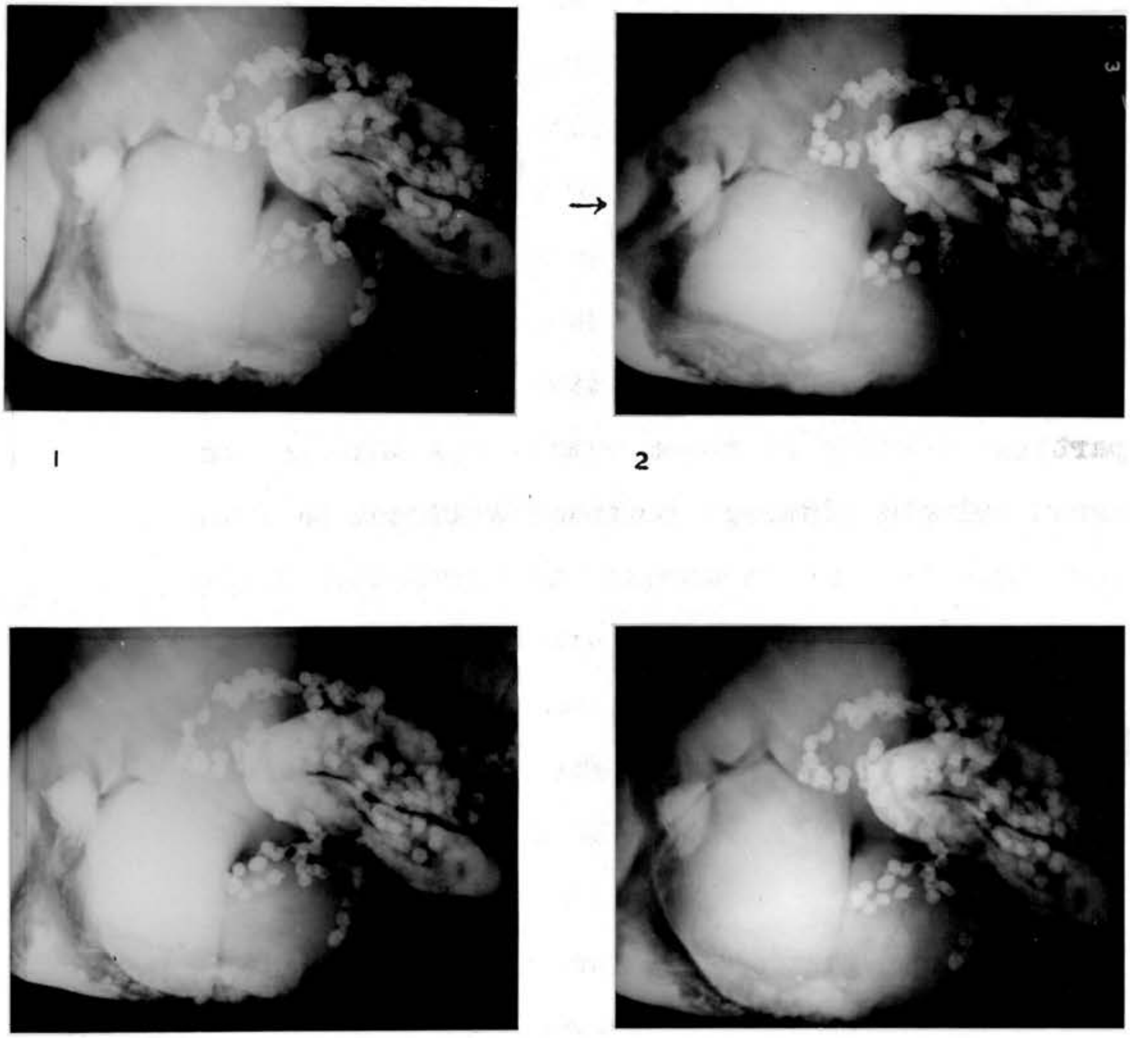


Fig. 31 Ruminoreticular contractions.
Subject aged 20 days, two hours after feeding.
Frame interval 4 seconds.
The reticulum, which is indicated by the arrow, is contracting in the second frame.

is certainly not the case that each reticular systole is preceded by periods of quiescence of the rumen as is not infrequently suggested.

While the pattern of activity just described is not stable it is sufficiently well defined to be clearly distinguishable from the gastric movements of the younger animals and it does not, in fact, develop for some weeks after birth. Unfortunately no particular study of these events was made in the youngest animals although indirect evidence is freely available for the occurrence of irregular, uncoordinated and even spasmodic movements within a few days of birth. The earliest more exact observations relate to a kid aged twenty days: this animal was fed by bottle, a considerable amount of milk reached the rumen and reticulum (fig. 31). When screened, the kid showed regular contractions of the reticulum occurring at intervals of approximately 30 seconds but these were not followed by the atrial contractions that would then have ensued in the adult: instead there was a slight contraction of the entire dorsal half of the organ which was in turn followed by a much more pronounced relaxation coinciding with the commencement of a forceful contraction of the ventral blind sac whose contents were ejected into both the reticulum and the dorsal sac. Between these movements the rumen appeared to be almost motionless.

This pattern of behaviour was gradually modified. At four weeks or thereabouts there is considerably more activity of the other parts of the rumen and regular alternations of contraction of the dorsal and ventral halves of the rumen are evident, but still without any sign of independent activity of the atrium. This in fact does not develop until some time about the sixth or seventh week of life and it will be recalled that the anatomical development of this part was similarly retarded. The onset of atrial contractions is delayed for varying periods in different animals but once it has occurred in any individual it is thereafter constant in that animal: its appearance does not seem to be directly correlated with the feeding habits of the kids for some of those greediest for solid fodder were among the last to develop this activity.

Further changes are relatively slight and an almost adult activity is present in animals as young as eight weeks. It is difficult to be categorical about the duration of the cycle at different ages for the figures vary so much at different sessions and are also influenced by such matters as the time since feeding and the onset of rumination. But if any general trend is evident it is a gradual increase in the length of the cycle continuing for some weeks before a greater stability is acquired: this may however show a slight reversal before maturity is reached.

A single example will be quoted. In one animal (13/53) the average intervals between reticular contractions were:-

at	5 weeks	90 seconds
	11 weeks	50 seconds
	15 weeks	43 seconds
	20 weeks	50 seconds

Discussion.

While much of what has been recorded here concerning the activities of the rumen and reticulum merely confirms the accounts of these events provided in recent years by several authors a more extensive reference must be made to the numerous additional and irregular contractions of the ruminal subdivisions since these do not find a parallel in the other descriptions. Fortunately there can be no question regarding the occurrence of the supernumary contractions in the animals used in this enquiry for not only were the irregularities consistently noted during the screening sessions but they are also conspicuously present in the serial films. On the other hand, the absence of frequent minor contractions in the stomach of the subjects of other investigators is no less well established for not only do most accounts make no mention of any significant irregularities but in many cases they provide tracings of the intraluminal pressure which depict a fairly rigid adherence to a simple and uniform pattern of behaviour. In these circumstances it is not easy to decide the significance of the contradictory results: several possible explanations may be mentioned.

The most obvious and perhaps the most attractive interpretation would regard the discrepancies as indications of a true species variation and while positive proof of this is lacking there are several factors which lend some support to the view. Most other investigators have used sheep or cattle for their work and the goat figures in comparatively few accounts. It was this species, however, which was selected by Czepa & Stigler for their studies and it has already been observed that these writers presented a rather confusing account of the rumino-reticular cycle which cannot be reconciled in many details with other descriptions: among other points of distinction they were among the few who reported independent activity of the blind sacs. Their inability to correlate ruminal and reticular activity may, it is now suggested, be connected with the variable performance of the rumen in this species. Magee's explanation of the same events is also rather confused and it may not be without significance that he too employed goats. These facts are at least suggestive and it will be recalled that the precedent for species variations in the rumino-reticular cycle certainly exists and is well examplified by the different nature of the reticular contractions in the sheep and the ox.

Alternatively, or perhaps additionally, there is the possibility that age variations explain the discrepancies. Unfortunately it is difficult to assess the probability of this since many have neglected to provide information bearing upon the age and breeding of their subjects. It has been shown that in the kid the adult type of cycle appears relatively soon after birth and it is probable that most workers have used animals of some maturity which would appear to exclude the likelihood of confusion arising on this score. It may be recalled that Phillipson used lambs in addition to adult sheep and as his findings for the two groups are in relatively close agreement, once the earliest stages are outgrown, it is probable that, except in the very young, age is of little significance. The existence of a third possibility - that different techniques may record quite different impressions of these movements was alluded to in the introduction and while no very firm conclusion is possible it would appear very desirable to settle the question which is one of obvious importance. Simultaneous recording of intra-luminal pressures with filming of the fluoroscopic screen is now a by no means unobtainable ideal and would provide a clear cut and unequivocal answer.

Turning now to the gradual evolution of the characteristic activities it must be admitted that it was unfortunate that a special study of the movement of the forechambers was not made during the first period of postnatal life. There is however the indirect evidence obtained during examinations of the abomasum which shows that these parts are active within a few days of birth. That this should be so may at first sight occasion surprise for in these very young milk-fed kids the rumen and reticulum can have no function to perform. It will be recalled however that it has long been known that in many species the stomach is active considerably before birth (e.g. Windle, 1940). This aspect of prenatal physiology has been studied in lambs by Duncan & Phillipson (1951) and while they were not rewarded with the sight of spontaneous activity in the laparotomised foetus too much importance should not be attached to this negative finding since in these circumstances such activity is inhibited in the adult animal. Stimulation of the gastric muscle or of the appropriate nerves elicited a variety of contractions according to the age of the foetus and at least demonstrated that the neuromuscular mechanism necessary for these activities has developed well before term.

Fig. 35 The omasum of a subadult animal.
It will be observed that the bulk of the contrast material is concentrated along the lesser curvature and where the lower pole projects clear of the rumen it will be seen that its shadow is poorly defined. Striation indicates the alternation of omasal lamellae and recesses.

The abomasum and reticulum are also identifiable.

The Omasum

Radiological Anatomy

General considerations.

The omasum of the small ruminants, unlike that of the ox, never reaches any great size in proportion to the total bulk of the stomach and throughout life it retains a rather elongated form. In the goat it lies immediately to the right of the rumen and in contact with the visceral surface of the liver while its lower end rests upon, and opens into, the fundus of the abomasum. The omasum is invisible in plain radiographs but when outlined by a contrast meal it is clearly shown (fig. 35): when quiescent the long axis is almost vertical and usually the anterior margin of its image corresponds to the sulcus omasi and is thus concave. The orientation of the omasum varies however with its own contractions and with the activities of other organs and a rotation about its long axis may conceal the sulcus from view. The typical radiographic appearance confirms the observations of Wilkens (1956a, b), who described in the embalmed sheep and goat a vertical disposition of the omasal channel with its entrance directly above its exit, but it disagrees with the description of Florentin (1953) who reported a more horizontal inclination.

The characteristic feature of the interior of

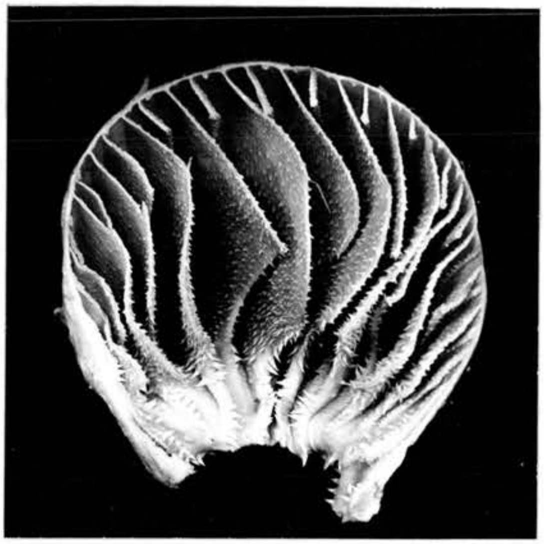


Fig. 36 Transverse section of omasum.

Fig. 37 Dorsal view at seven weeks. Note the position of the omasum and the appearance of the alternation of the lamellae and recesses.

the omasum is the presence of a large number of laminae of different lengths which occupy most of the available space: these arise from the greater part of the wall and converge upon but do not reach the anterior border along which the conducting channel runs (fig. 36). The alternation of these folds with the food-filled recesses gives the organ a striated appearance, best seen in the dorsal view (fig. 37), and their absence in the region of the omasal sulcus permits a greater concentration of food in this part, with a consequent increase in the density of the image.

Postnatal development.

In its postnatal growth the omasum tends to lag behind the other chambers of the stomach and it is known that this delayed response is due to the need for the stimulus to development provided by the presence of roughage in the diet (Trautmann, 1932). While this is lacking there is almost no increase. During the neonatal period the body of the omasum is rarely seen in radiographs for the milk flows directly through the sulcus into the abomasum: if a little of the feed adheres to the omasal mucosa the organ appears as an irregular shadow centrally placed in the intra-thoracic part of the abdomen at about the level of the eighth rib (fig. 49). In the dorsal view it is seen to lie to the left of the spine. At three weeks the rumen has expanded sufficiently to carry the omasum to the midline but the organ itself has grown little and a material enlargement is not apparent for another one or two weeks. At six weeks it is more conspicuous and lies predominantly on the right (fig. 22). Its rate of increase is accelerated during the next few weeks and at nine weeks (fig. 23) it is quite large and shows a conspicuous development of the internal laminae, but it remains in the same general position within the abdomen.

Further growth of the omasum proceeds regularly and is accompanied by a leisurely migration to the right, brought about by the expansion of the rumen and reticulum, and by a slow descent in conformity with the proportionate decrease in the dimensions of the abomasum; by five months the organ resembles that of the adult and the only changes that now occur are in keeping with the general increase in the size of the animal. The adult organ occupies a position much as described by Wilkens, lying under cover of the eighth and ninth ribs and with its lower pole level with the chondral attachments of these bones (fig. 30a).

Omasal Motility.

Previous literature.

The mechanics of the omasum have been less intensively investigated than those of the preceding gastric compartments, possibly because of the more difficult access to the organ and also because its activities are of a less obvious nature. The methods employed in these studies have been palpation of the interior, the registration of the intra-luminal pressure and fluoroscopy. The first two procedures have been used in the ox in which a fistula may readily be created to provide access for the introduction of the hand or of recording balloons, while the smaller species have been used for radio-graphy. Direct inspection of the intact or incised organ in the laparotomised animal (Mangold & Klein, 1927; Dukes & Sampson, 1937) has given largely negative results.

Wester (1926) recorded the pressure changes in the lumen of the bovine omasum and he described a sequence of three pressure waves related to each double contraction of the reticulum: he interpreted the first two as being peristaltic in nature and the third as antiperistaltic. The results of Schalk & Amadon (1928) did not correspond exactly and they reported more sluggish and irregular changes which they regarded as being mainly due to variations in tonus: they emphasised a point confirmed by most later workers, namely that the second reticular con-tration is followed by a fall in intra-omasal pres-sure with a consequent aspiration of ingesta.

Phillipson (1946) dissented from this view regarding the omasum as playing a purely passive role. Balch, Kelly & Heim (1951) studied the matter more intensively, paying particular attention to the opening of the reticulo-omasal orifice. They reported a slow rise in the pressure within the omasum, commencing before the reticular contraction, and suddenly falling away at the time of the second reticular contraction before recovering for a spell: at the time of the peak of reticular systole there was a drop in the pressure at the orifice followed by a powerful contraction. On palpation they found the orifice loosely open during the greater part of the rumino-reticular cycle but tightly closed at the onset of contraction of the reticulum. They believed that the ingress of ingesta occurred during the final stage of reticular contraction and that the passage of the material into the abomasum occurred in two stages with a constriction across the bridge of the omasum preventing an uninterrupted flow; in this conclusion they are at one with Wester. They further suggested that the omasum acts as the pacemaker for the ruminoreticular cycle.

Brunaud & Dussardier (1953b) confirmed the regularity of the omasal activities and stress their association with those of the first two chambers, noting three contractions of the omasum to each one of the reticulum and they point out that where a breakdown in this rhythm occurs it is generally the reticulum which is 'at fault': the omasal regularity seems to be the more fundamental and since it persists when the reticular movements are suppressed they support (without quoting) the suggestion of Balch et al. Habel (1956) noted that if the 'pump' interpretation of omasal activity is correct then a reciprocal and efficient valvular action is necessary at the exit from the omasum, a region neglected in all accounts. It is convenient to mention at this point the reports of Akssenowa (1932) and of Trautmann & Schmitt (1933) in which they described a reflux of milk from the abomasum to the fore-chambers: this they believed to be a normal occurrence and it implied that the folds guarding the omaso-abomasal orifice will permit the retrograde flow of the abomasal contents.

In the first radiographic description of the ruminant stomach Czepa & Stigler (1926) stated that they were unable to recognise any omasal activity: this view is repeated with rather vague qualifications in their second paper (1929) in which they suggested that the omasum acts merely as a filter. Magee (1932) was also unable to detect any intrinsic movement but Phillipson (1939) described important changes. The most conspicuous occurred during reticular contraction when the organ is carried downwards and forwards and, relaxing, fills with ingesta. Its return to its former position is followed by changes in shape which appear to squeeze out a blob of food. Passage of material into the abomasum was said to occur at other times too, suggesting that secondary contractions occur unrelated to reticular activity. In a recent communication by Benzie & Phillipson (1957) other movements are stated to occur but their exact nature is left rather vague and it is warned that changes in orientation may simulate intrinsic activity. They concluded that the expansion of the omasum following reticular contraction accounts for its filling while its horizontal disposition at this stage results in the entry of the material into the interlaminar recesses.

Observations.

The fluoroscopic study of the omasum is apt to be disappointing: the image of the organ is often not particularly clear as it is superimposed upon other opaque parts; the changes in form are not of great magnitude; the less obvious alterations tend to be irregular in their occurrence; and attention is distracted from the more definite movement that accompanies reticular contraction by the more strik-

Fig. 3b Single frame extracted from a ciné sequence and showing the passage of milk along the sulcas omasi. Little of the fluid penetrates the inter-lamellar recesses.

It will be observed that the abomasum follows the abdominal floor and, dipping down behind the saphoid, is strongly indented ventrally by this structure. The subject was aged four months.

The sequence showed little activity and a longer extract is not presented.

ing activity of the latter part. Much of the following account is therefore based upon the serial exposures. Plates 3, 4 and 5 may conveniently be consulted at this juncture.

The passage of milk through the omasum is the same at all ages. It follows the lesser curvature almost exclusively (fig. 38) and only traces reach the interlaminar spaces, although once here they may persist for lengthy periods (fig. 18). The entry of other ingesta is less easily seen. At times it is possible to determine that there is a movement of ingesta into the omasum during contraction of the reticulum but this is not an invariable accompaniment of this process for on occasion the omasum may not appear for an hour or more following the administration of the experimental feed although the rumen and reticulum have been active. It is, of course, impossible to see whether the omasum experiences alterations in form as well as of position when the opaque material has not yet reached it and later when this chamber is outlined it is not easy to decide which contractions are accompanied by the passage of more ingesta. There is however a strong suspicion, to put it no higher, that the cycles which are not associated with the intake of the feed are marked by considerably less change in the form of the omasum: that movement illustrated in figure 34, plate 4 appears to be of this nature. A fuller series of the same events but with the probable influx of food is shown in figure 33, plate 3.

During the contraction of the reticulum the omasum is carried downwards and forwards, the lower pole being most affected as it is attached to the abomasal fundus which is displaced to occupy the former position of the reticulum. In consequence of this displacement the omasum comes to occupy an oblique position but the horizontal disposition described in certain accounts has not been encountered. The change is accompanied by a considerable increase in the curvature of the organ (frame 13, fig. 33; frame 2, fig. 34) and by an expansion of the upper extremity and a less obvious contraction of the lower one. As the omasum reverts to its former position it appears to shorten somewhat and a deep indentation makes its appearance on the greater curvature towards the lower pole: the upper part at first shows little change and it is difficult to place a limit upon the duration of its expansion. The contraction of the lower part persists for some time and on occasion it appears as though the constriction gradually extends distally before it is slowly effaced by a wave of relaxation. When the lower part is contracted it may be possible to detect the escape of a fraction of the omasal contents into the abomasum.

Changes in the form of the omasum occur during other phases of the ruminoreticular cycle. They are sometimes concerned, as Phillipson (1939) noted, with the passage of food into the abomasum but there is no evidence that an intake of food from the reticulum occurs at any other time than that just described. These other changes are relatively minor in their expression and unpredictable in their occurrence. One common appearance is an irregular shortening and lengthening of the organ while it maintains its usual upright position: the change in length may amount to about 10 or 15% of its length at a rough estimate and with this there may be an alternate expansion and relaxation of each pole in turn: the movement may be accompanied by a rotation about the long axis of the organ and because of this it is impossible to determine whether there is any general change in capacity. One such cycle - if this term does not suggest too great a regularity of occurrence - is shown in figure 39, plate 5.

Other changes by no means always follow the one pattern but usually they consist of some combination of the same features - variations in length which are slow in execution and often of prolonged duration and very irregular alternations of expansion and contraction, restricted in many cases to the one pole.

The omasum cannot be properly studied in very young animals. In those aged six weeks and more it was impossible to detect any alteration associated with increasing age but as the movements were so irregular the possibility cannot be entirely excluded.

Discussion.

Until relatively recently attempts to interpret the motor activities of the omasum were hampered by some confusion regarding the essential function of this chamber and even now it cannot be said that the matter is settled to universal satisfaction. Formerly it was believed that its most important if not sole function was to retain and to secure by mechanical means the further breakdown of the larger particles of food, combining in this way the action of a filter and a mill. The evidence for this view of its purpose was largely circumstantial: large pieces of ingesta are relatively uncommon, though by no means unknown, in the abomasum and the material within the omasal interlaminar recesses does show a gradation in size on passing from the dorsal to the ventral extremity (e.g., Becker, 1937; Favilli, 1937). No one has succeeded in demonstrating or explaining how this breakdown takes place and attempts to detect an independant activity of the laminae have uniformly failed (e.g., Dukes & Sampson, 1937). The experiments of Trautmann & Schmitt (1935) who sought confirmation of this function by creating an opening between the rumen and the abomasum are not decisive since the food that passes through this fistula not only by-passes the omasum but also escapes prematurely from the rumen. More recently a more favoured theory has ascribed to the omasum a pumplike action assisting the flow of the ingesta from the ruminoreticulum to the abomasum, and this interpretation receives support from the pressure tracings, especially those supplied by Balch and his colleagues, and from the present radiographic description. It is now possible to form a tolerably clear view of the mechanism involved. The omasal orifice opens during the later stage of reticular contraction and the ingesta pass through into the simultaneously relaxed upper portion of the organ: the orifice is then closed and a general tightening of the adjacent part forces the semifluid material down into the body of the organ where it is retained by the constriction that appears about the waist. The upper pole may now relax without risk of reflux of the greater part of the contents which can be passed on into the abomasum at leisure by a tightening and squeezing of the middle and ventral sections. This ejection proceeds without reference to the motility of the first two chambers if the irregular activities of the omasum are performed for this purpose, as seems to be the case: certainly they appear to be well adapted to 'milking' the food distally.

In discussing this process it is usually claimed, frankly or by implication, that the ingesta are first drawn into the omasum by an expansion of its upper part following the relaxation of the muscle of the wall and Hoflund (1940) has actually recorded a negative pressure within the lumen. The literal interpretation of pressure readings is known to be dangerous (Quigley, 1947) and it may be doubted whether in fact a thin-walled organ such as the omasum, which may be likened to a balloon, would expand in this way following the reduction in muscle tone: it would appear more likely that the omasal role is purely passive and that it is the increase in pressure on the reticular side of the orifice which alone is responsible for the filling of this organ.

It is not of course suggested that the mechanical is the sole function of the omasum for it is also able to absorb water and certain constituents from the fluid within its lumen (Garton, 1951) and this, rather than mere deposition, accounts for the progressive increase in radiodensity of the material contained within the recesses.

That none of these rather diverse functions is vital to the economy of the animal could be presumed from the natural absence of this organ from the otherwise similar stomach of the related Tragulina and is confirmed by the absence of any alteration in health following upon its removal (Trautmann 1933b); nonetheless it is not without interest that in these circumstances it generally reforms, suggesting that perhaps after all it has some important if not vital role.

Another point of some morphological interest may be noted in passing. It relates to the transverse constriction that develops at the waist of the organ, which according to some interpretations of the homologies of the ruminant stomach (see Pernkopf, 1931 & Torgesson, 1942) corresponds to the position of the antral sphincter of the simple organ. It cannot be said, however, that there is any special differentiation of the circular muscle of the omasum in this position.

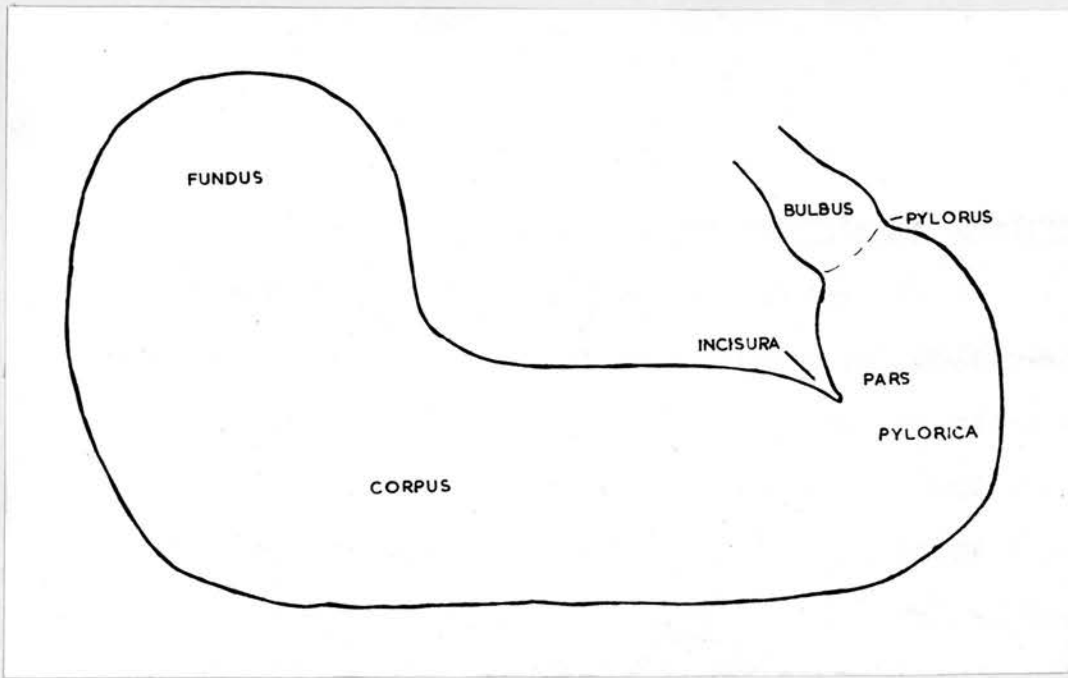
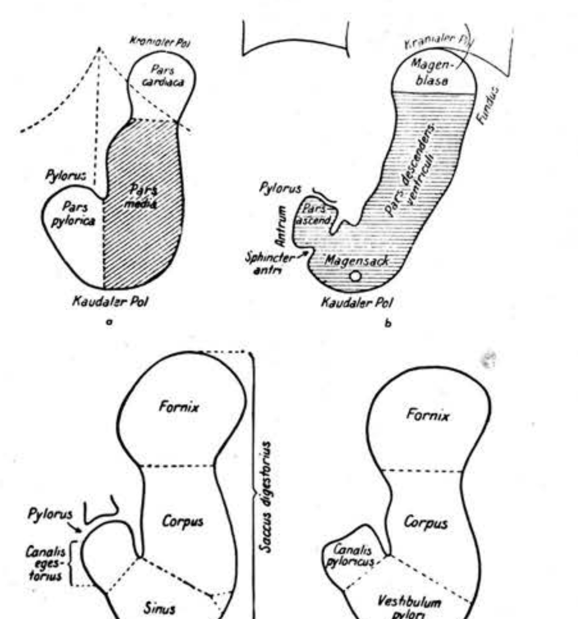


Fig. 40 The parts of the abomasum. See also figures 43 and 44.



56. Nomenklatur des Magens nach Holzknecht (a), Groedel (b), Forssell (c) und Aschoff (d); nach Katsch).

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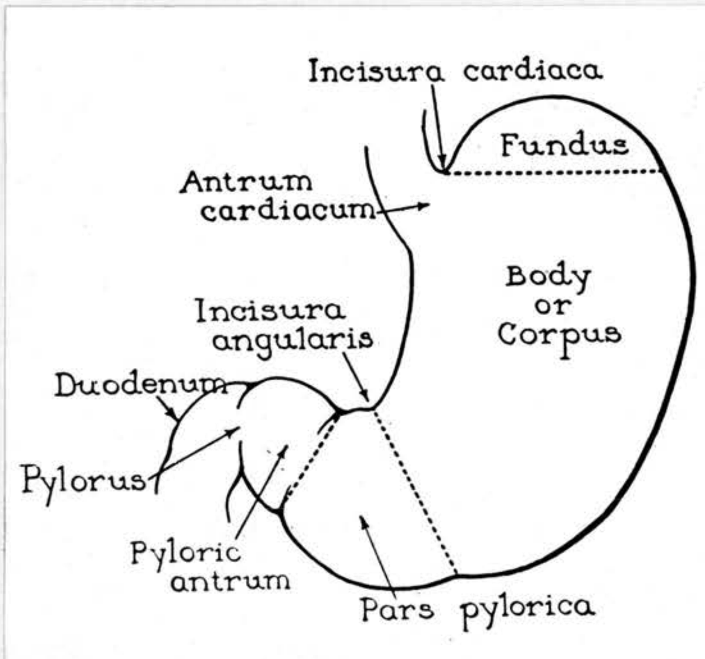


42

Figs. 41 & 42 The parts of the human stomach according to various authors.
Fig. 42 from Alvarez after Lewis, fig. 41 from Catel.

The Abomasum

Radiological Anatomy

General considerations.

In its general form (fig. 40) the abomasum resembles the simple stomach of man and other mammals although unlike these it is derived only from the more distal section of the primitive gastric spindle, the fore-chambers arising more proximally (Pernkopf. 1931: see his Schem. Abb. 9). The living organ shows a greater regional differentiation than the post mortem specimen and it is necessary to supplement the usual descriptive terms by borrowing some of those used by the radiologist in the description of the human stomach. Unfortunately the latter terminology is in so confused and contradictory a state that an initial examination of questions of nomenclature can hardly be avoided.

The primary division of both the abomasum and the human organ into a large sac-like proximal portion and a narrower, more tubular section leading to the pylorus presents no problem. The former part may be divided into a fundus and a corpus (figs. 40-42), the parts of the two organs being analogous rather than true homologues. The remainder of the organ is more complex. Retzius (1856) termed the whole region the antrum (pylori) and while many have accepted his definition others

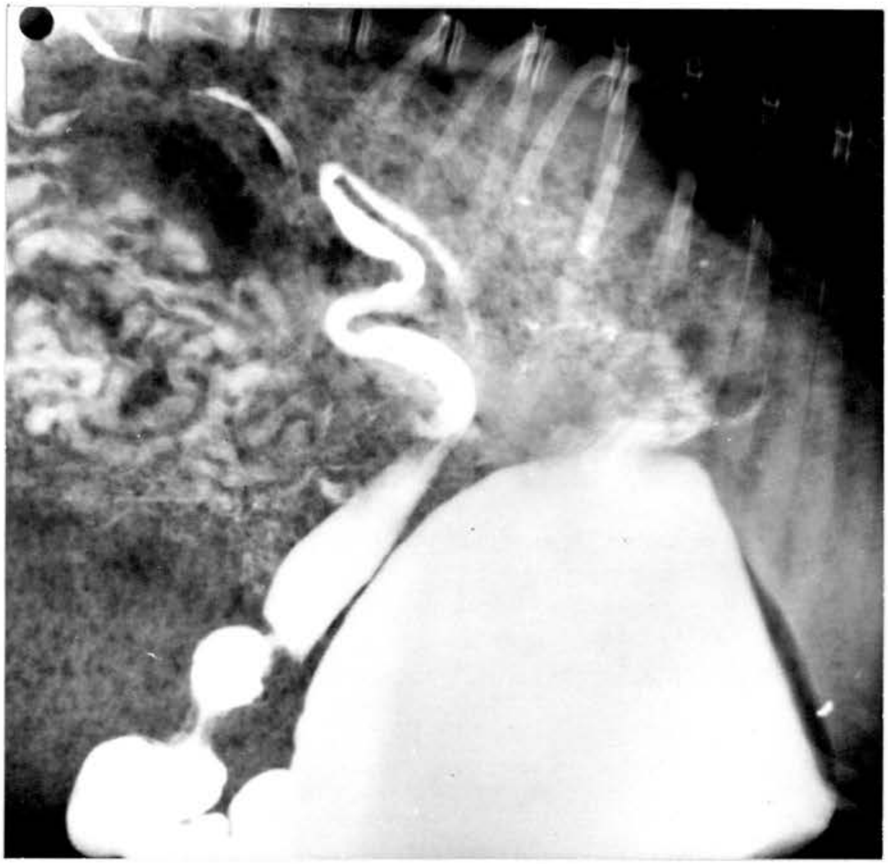


Fig. 43 Radiograph of a subject aged nine weeks. The animal was recumbent and the gas lies against the cranial margin and not in the fundus as in the standing position. Commonly at this age the organ possesses a more tubular form.

The pyloric part is active and permits ready identification of the sinus, antrum, pylorus and incisura angularis: the torus is less conspicuous. The duodenal bulb is well filled and the complex convolutions of the flexura portalis are visible while patches of contrast lie in the succeeding portion. Loops of small intestine and the omasum will also be recognised.

have followed Luschka (1863) in restricting the application of this term to the immediately prepyloric region. The term thus acquired a certain ambiguity and Müller (1921) therefore proposed its abolition: Forssell (1913) introduced the expressions sinus and canalis egestorius for the oral and aboral parts of the region and although these have gained a certain currency, among radiologists in particular, they have not been universally accepted. A selection of the systems in present use is shown in figures 41 and 42. The system adopted here (fig. 44) is yet different: the term antrum is retained in its more restricted sense since the alternative canalis egestorius is too cumbersome for repeated mention and the usual abbreviation to canalis tout net is liable to be confused with the true pyloric opening to which it lies adjacent and to which separate reference must sometimes be made. The expression 'pars pylorica' has seemed the most logical of the more inclusive terms and certainly preferable to the other common alternatives, 'pars ascendens ventriculi' or 'transverse stomach', which are inappropriate for general use whatever their merits in human anatomy.

It is a matter of dispute whether these subdivisions possess any real anatomical foundation. Pernkopf (1929, 1931) who has made a most extensive investigation of the comparative anatomy and embry-

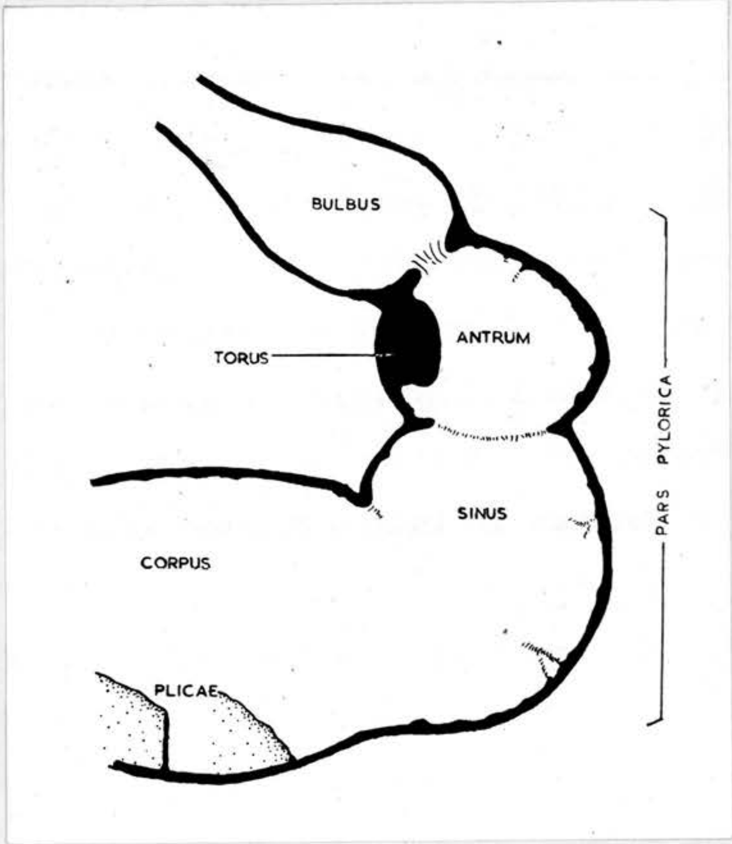


Fig.44 The subdivision of the pars pylorica seen in schematic section. In general the terminology employed follows that used by Lewis (see fig. 42).

ology of the stomach maintains that the various regions and features described by Forssell and others are not based upon any muscular differentiation and represent merely fleeting functional forms but even if this contention is largely true, and it cannot be accepted in its entirety, they are of such regular and consistent recurrence that they cannot be ignored in any consideration of the functional anatomy of the stomach. Certain aspects of this difference in interpretation will receive further consideration at a later stage: a full discussion of the problem is most capably presented in the undeservedly neglected work of Torgerson (1942). The formal description of the radiological appearance of the abomasum may now be undertaken.

The abomasum is the most plastic of all the chambers of the ruminant stomach for not only is it at times the seat of great activity but being thin-walled it is liable to deformation by the pressure of the adjacent viscera. It has already been indicated that the fundus and corpus are of arbitrary distinction: in theory the fundus projects dorsally above the omaso-abomasal orifice but the mobility of the abomasum is such that this cul-de-sac corresponds to no sharply defined portion of the organ. The fundus is dome-shaped and may reach high into the abdomen: it occupies the s pace between the rumen and the reticulum and extends behind the omasum. It is attached to all these organs and its position is thus influenced by their activity: its connexion is greatest with the omasum with which it communicates through the extensive ostium omaso-abomasicum. The fundus normally contains a bubble of air and this serves in the absence of a contrast feed to indicate its position in radiographs.

The corpus extends dextro-caudally from this region, in contact with the abdominal floor between the ventral sac of the rumen and the liver: it tapers to its junction with the pars pylorica. Both the fundus and the first part of the corpus are marked internally by a series of mucous membrane folds or plicae - upwards of a dozen in number - which arise about the entrance and course spirally over the wall before gradually subsiding in the distal part of the body. These folds are often prominent in radiographs (fig. 51) but occasionally they may be a source of confusion if they are apparent only where they cross the lower border since the interruptions they produce in the shadow strongly resemble the passage of weak peristaltic waves (fig. 53).

The junction of corpus with pars pylorica is marked by a flexure, the incisura angularis, which indents the dorsal margin: to this a ridge corresponds internally. The reflected pyloric part extends

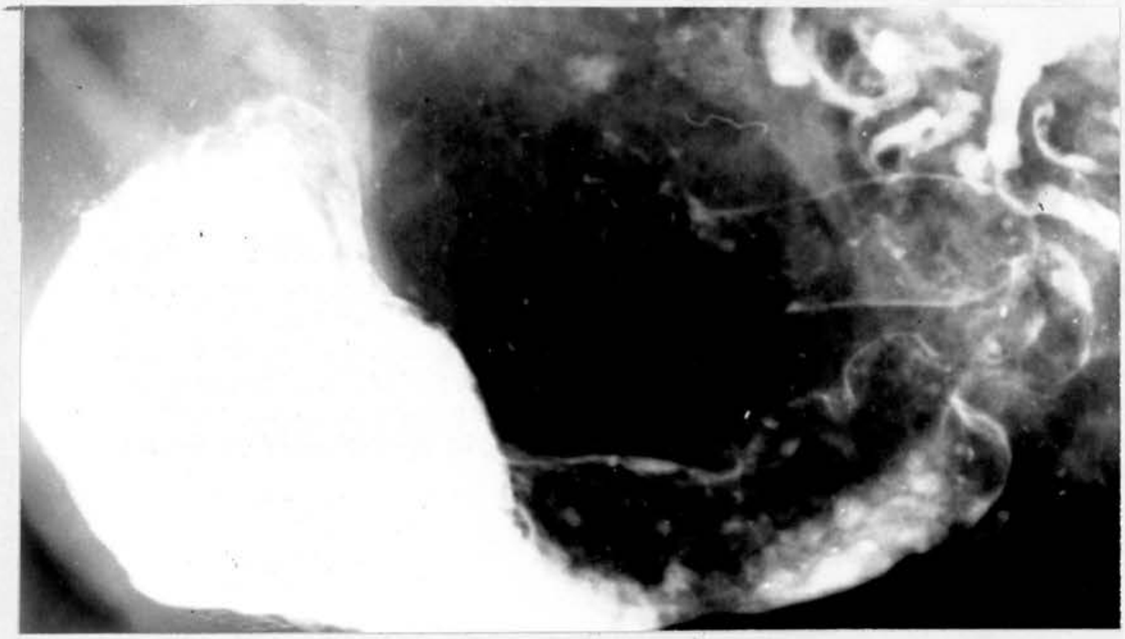


Fig. 45 In this film the posterior half of the abomasum is occupied by gas and a thin layer of barium adheres to the mucosal lining producing a double contrast effect. It displays the indentation of the torus pylorica and the elongated form of the antrum in mid-systole. The outline of the antral cavity at the base of the torus is faintly suggested.

Note also the peristaltic indentations. It is not easy to account for the form of the anterior part of corpus and fundus but probably the depression is caused by the pressure of the anterior dorsal sac of the rumen. The subject was 32 days old.

cranially and to the right, joining the duodenum under cover of the liver. It is considerably narrower than the preceding sections and while it has a basically tubular form (figs. 44 & 45) it shows a variety of shapes depending on the activity of the muscle in its walls, for being of more robust construction its movements are more forceful than those of the preceding sections. Frequently it appears to consist of two parts - a proximal sinus and a distal antrum. The sinus commonly shows peristaltic activity while the antrum is the seat of systolic contractions, indicating that the division is of functional significance.

The abomasum communicates with the base of the duodenal bulb through the pylorus: this is a relatively short canal and when closed it is not always visible even when the parts it joins are distended with opaque contents. Commonly in these circumstances it appears as a tenuous thread (frame 10, fig. 63, plate 7). When dilated it is several millimetres in width and may be marked by longitudinal striations which indicate the presence of folds in the mucosal lining (frame 20 of the same figure). Despite the warnings sometimes expressed there seems to be little difficulty in recognising the fully relaxed pylorus.

There exists in the ruminants a permanent torus

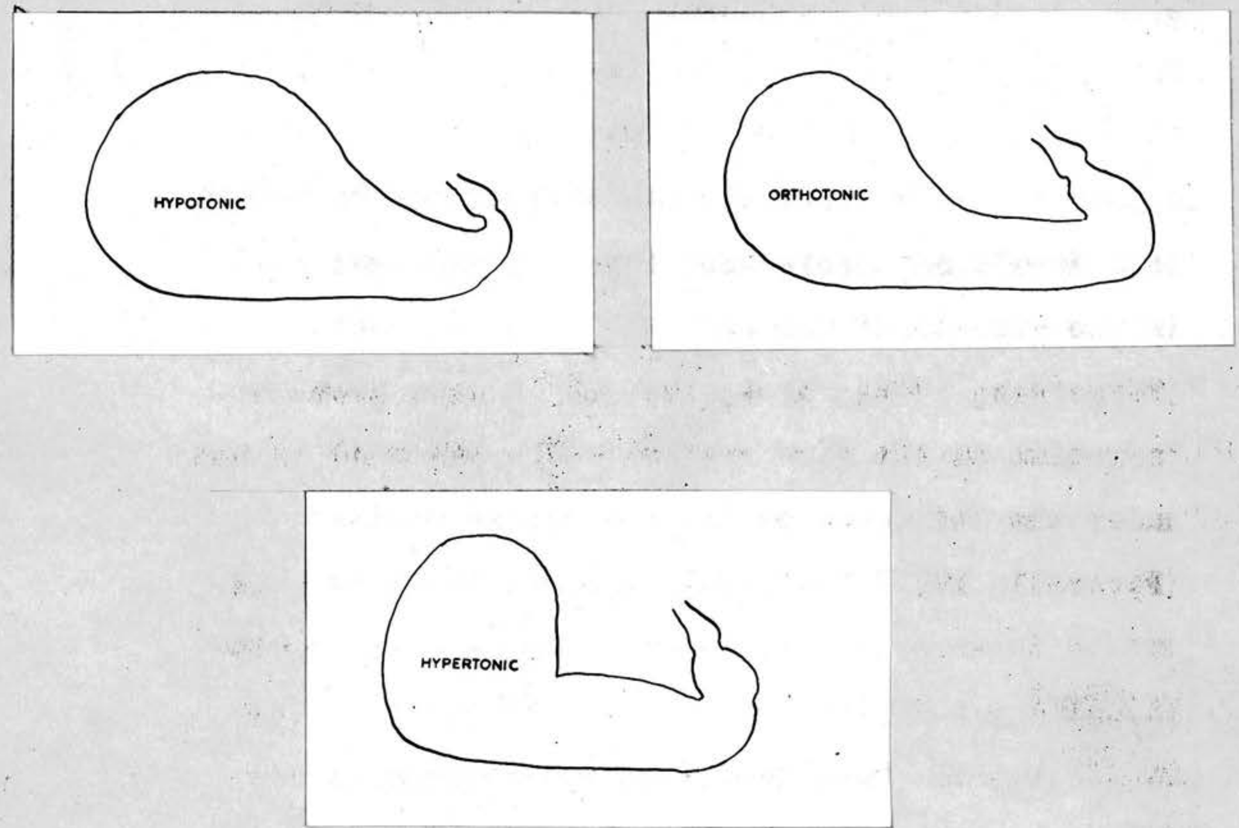


Fig.46 a, b & c. The effect of muscle tone on the shape of the abomasum.

pyloricus, a pad projecting into the antral lumen from the lesser curvature before and extending to, the pylorus. This formation has a characteristic appearance in radiographs and corresponds to a much less developed muscle knot found at the same site in the stomach of man and many other species (Torgerson, 1942; Keet, 1957). A more prominent formation in the same region may be produced in man under the influence of the muscularis mucosae (Forssell, 1937) but independant activity of this muscle layer is not pronounced in the kid: occasionally a plexiform pattern is developed in the fundic region which doubtless corresponds to the adherence of the agent to mucosal ridges: examination of the fresh viscus will not normally reveal their presence. Minor indentations of the sinus and antrum are more common and are probably produced in the same way (fig. 67).

A very potent influence on the form of the stomach is the general muscle tone (fig. 46). The hypotonic abomasum (fig. 47) is flaccid, pyramidal and dorsally enlarged while the hypertonic organ is low, tubular and often sharply bent about the middle of the corpus: intermediate shapes naturally occur but there seems to be little point in cataloguing their great variety by reference to fanciful resemblances to common objects since they are subject to

Fig.47 A hypotonic abomasum greatly distended with air and almost globular in form. A second meal lies above the first in which the barium (a coarse and unsuitable preparation was used) has settled from suspension. Observe also the ruminal gas and traces of contrast in omasum and reticulum. The position of the gas bubble lying in front of the omasum cannot be identified confidently - it may lie below the cranial pillar of the rumen.

sudden and drastic alterations in shape.

Postnatal development.

In the recently fed neonatus the abomasum determines in large measure the position and relations of the other abdominal organs (fig. 48). But since at this age the abomasum functions very much as the simple stomach of other species, it is at times almost empty and then naturally its relations alter. Here only the partially full organ is described: some account of the process of filling is presented later. The moderately distended abomasum (figs. 49 & 50) rests firmly upon the abdominal floor with its long axis extending caudally and somewhat to the right: it is separated from both flanks by a considerable space corresponding to the liver and small intestine to the right, and the rumen and small intestine to the left. Anteriorly it lies below the reticulum and in extensive contact with the diaphragm while its caudal limit reaches the level of the fourth interlumbar articulation, although the usual flexure carries the pyloric part forwards from this in relation to the dorsal or lateral face of the corpus. Usually this section lies against the deep surface of the liver. Further increase in size brings the abomasum into extensive contact with the left flank

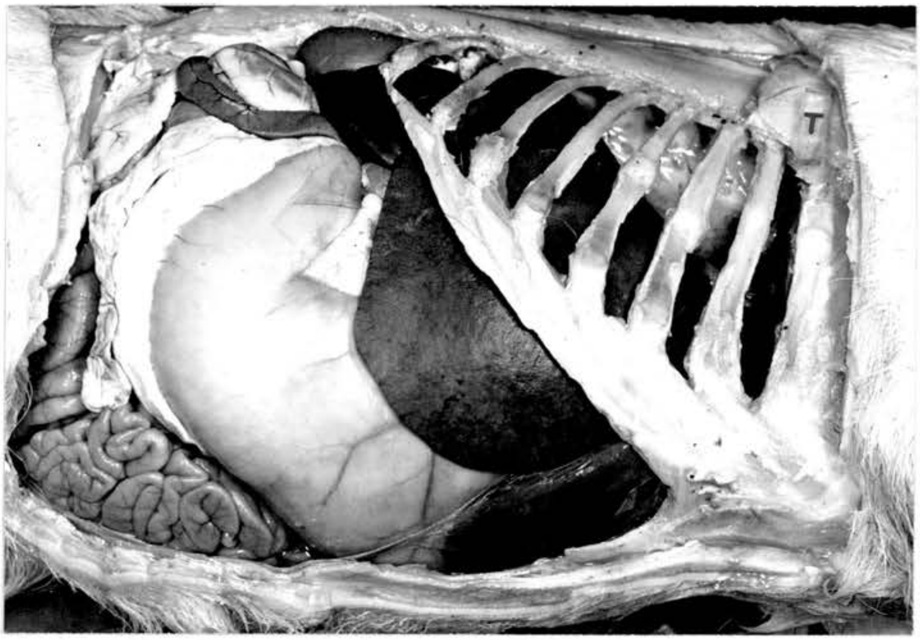


Fig.48 Dissection of the right flank of a kid aged 4 days. Note the large volume of the abomasum and the extent of the liver beyond the margin of the costal arch. The kidney and part of the horizontal loop of the duodenum are also visible while the small intestines occupy the rear part of the abdomen.
The falciform ligament may also be distinguished proceeding from the umbilicus to the umbilical fossa of the liver.

since to the right the firmly anchored liver resists displacement (figs. 51 & 52).

The foregoing description refers to the typical arrangement but deviations from this are common and may appear suddenly in animals kept under continuous fluoroscopic observation. One variant is the vertically elongated abomasum (fig. 53): this appears to be common in the calf during and after feeding (Benzie & Phillipson, 1957) but it is less frequently encountered in the kid and then apparently without this association. More common is the large globular and flaccid organ which occupies the greater part of the abdominal cavity: sometimes this is seen following excessive ingestion of air but where there is no obvious excess of gas it may be indicative of emotional distress.

Appearances soon change once the rumen commences its development for as the absolute size of the abomasum increases slowly, its relative bulk decreases. At the age of three weeks (fig. 17) when it is full and relatively inactive it may extend as far caudally as before, but as it empties it contracts in a forward direction: when activity is greatest, which is usually some time after the ingestion of a meal when evacuation is well under way, it extends little behind the most caudal part of the last rib. Activity at the age of two to

Figs. 49 & 50 Lateral and ventral views of the abdomen of a kid 3 days old. The abomasum contains a small feed administered 25 minutes previously.

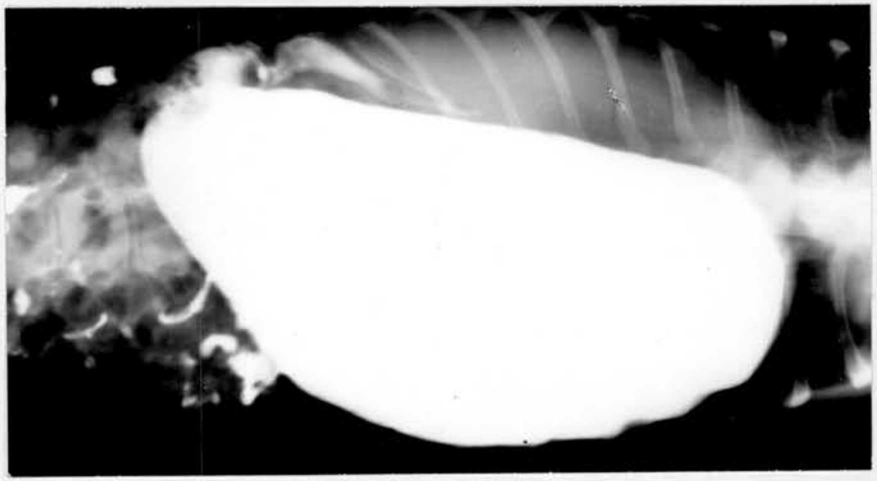
In the lateral view note the omasum and the "woolly" outline of the abomasum. The indentation of the lower margin is formed by a plica crossing the wall at this point. Cranially the liver separates the abomasum from the diaphragm. Numerous collections of gas lie in the small and large bowel.

The ventral film shows the abomasum separated from the right abdominal wall by the liver cranially and from the left wall by the rumen cranially and the small intestine caudally.

four weeks is very pronounced and there is associated with it much variety of appearance which particularly affects the pyloric part (fig. 54).

At six weeks the abomasum is relatively smaller and it is clear that whereas in the younger animals this organ determined the position and fate of its neighbours, it is now itself moulded by the rumen and reticulum (fig. 56). The latter organ usually curtails the former extensive contact of the abomasum with the diaphragm while the relative diminution of the liver permits a forward migration of the pyloric part so that the organ as a whole lies more transversely and does not extend behind the second lumbar vertebra (fig. 24). The lateral view shows that the fundus is confined to the more ventral part of the abdomen and no longer extends as far dorsally as formerly.

These changes continue during the next few weeks: a more tubular shape is now permanent and the abomasum rarely exhibits the signs of great activity that were once its most characteristic features. The more transverse disposition persists (fig. 57) and the flexure lies below the second lumbar vertebra with the pylorus consequently lying well in front of the last rib. Variations in position naturally occur and the abomasum may even lie completely transversely, in form and sit-



Figs. 51 & 52 Lateral and dorsal views of abomasum of week old kid. In the former observe the extent of the abomasum and also its plicae and the circular shadow of the pyloric antrum: this is almost separated from the remainder of the organ. The caecum is filled with gas but the ansa proximalis is well filled although little food lies in the small intestine. The omasum is barely visible.

In the other view the abomasum lies in contact with left flank and cranially displays costal indentations. The duodenal bulb lies to the right of the corpus and in front of this there is the denser shadow of the liver. This film was obtained shortly after feeding.

uation not unlike the simple stomach of the dog (fig. 58), but this extreme appearance is unusual and transitory. In older animals the abomasum becomes more and more restricted to the anterior part of the abdominal cavity. The fundic part remains insinuated between the two forechambers and while the pyloric part is freer it is as a rule to be found below and lateral to the omasum: its exit lies approximately level with the anterior part of this organ (fig. 28). At four months it is evident that the rumen is weighing upon the abomasum, distorting its form and limiting its range of movement, and the same may be said of the later stages. In fact little alteration is noted in the older animals in which the organ occupies a relatively insignificant part of the abdomen.

Abomasal motility.

Previous literature.

There are relatively few published accounts of abomasal activity and of these the more informative are based upon radiographic studies of the smaller domestic species. The first description of importance is by Czepa & Stigler (1926). These authors were unable to detect any intrinsic activity of the fundus and corpus of this organ but they reported that the pyloric part was at times the seat of very vigorous peristaltic move-

Fig.53 The abomasum of a kid aged 10 days one hour after feeding. An unusual amount of air remains in the fundus and this part reaches far higher in the abdomen than is usual. Note also the ruminal gas shadow and partially overlying this, at the junction of the caudal margin and ruminal meniscal level, is the denser shadow of the right kidney. Coils of small intestine are also evident.

ments: they remarked that the distinction between these functionally defined regions was emphasised by a deep constriction which almost separated the active from the inactive part. During the bouts of activity the peristaltic waves appeared in regular succession, at intervals of seven or eight seconds and their progress was such that four were usually simultaneously visible. In a later communication Czepa & Stigler stated their belief that the intrinsic movements of the abomasum were independant of the activities of the other gastric compartments.

Magee (1932) reported very little movement of this chamber.

Schalk & Amadon (1928) examined this organ in the ox and prepared tracings of the variations in intra-luminal pressure but it appears probable that their records were influenced by changes passively experienced by the abomasum during the movement of other parts. The validity of certain of the findings of Kryzwanek & Quast (1937) admits a similar doubt although they did record unequivocal evidence of peristalsis of the pyloric part. In a study conducted in laparotomised sheep Dukes & Sampson (1937) observed diastole and systole of the body of the abomasum in addition to powerful peristalsis of the pyloric extremity. They were at pains to emphasise

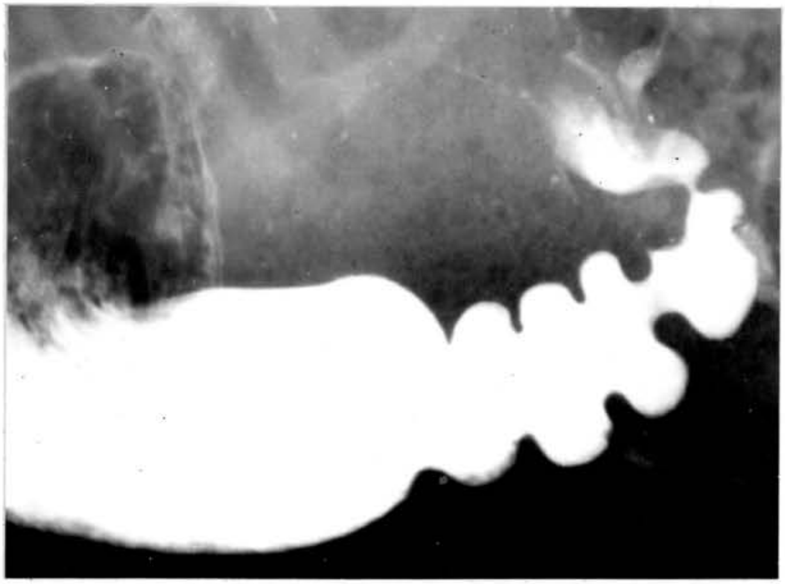


Fig.54
Hypertony and Hyperperistalsis of the pars pylorica of the abomasum. The peristaltic waves continue to the pylorus and one bisects the outline of the torus pyloricus. The series from which this illustration was enlarged is reproduced facing page .

that these peristaltic waves continued without interruption to the pylorus itself.

The description of Phillipson (1939) is mainly based on radiographic observations. He described occasional peristaltic waves coursing over the body and much more forceful contractions of the distal extremity which appeared to be stimulated by the tipping of food into this part of the organ during reticular contraction. Balch, Heim & Kelly (1951) reported - in the cow - slow peristaltic movements with peaks of intensity recurring every 2-4 minutes Their technique was based on pressure recordings and they were thus unable to specify the sites of activity. The description of Brunaud & Dussardier (1953b) did not add much that was new: these authors suspected, but could not be certain, that a connexion existed between the contractions of the reticulum and those of the abomasum.

Abomasal activity in the young kid was described by Dyce, Merlen & Wadsworth (1953). The movements were said to be most vigorous in animals aged about 3 weeks and later appeared to fall off in force. In addition to the familiar peristaltic waves antral systoles were reported but the relation between the two movements was not determined.

Benzie & Phillipson (1957) described slight rippling movements of the ventral surface of the body

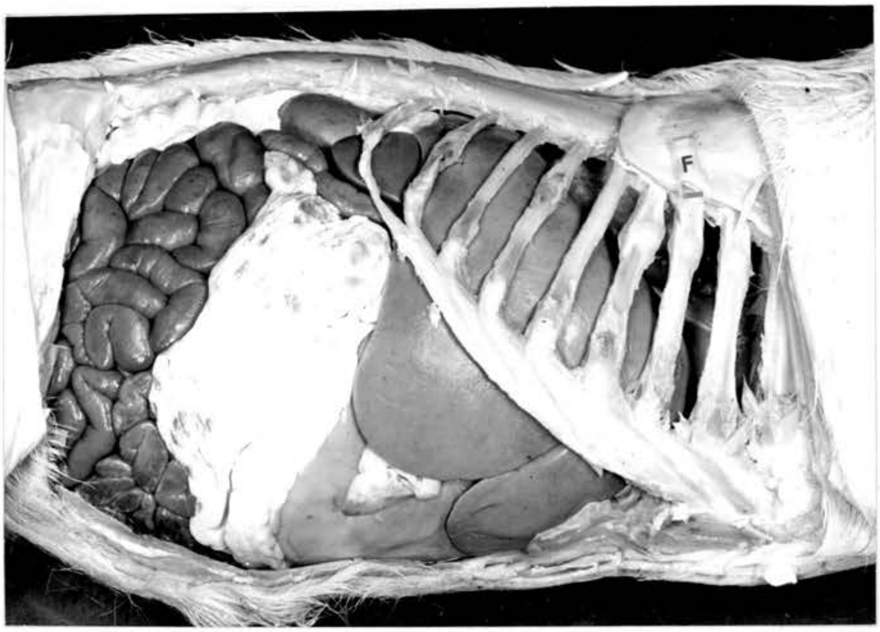


Fig.55 Right flank dissected at 2 weeks. The abomasum is only partially full and extends less far caudally than is often the case. The liver is slightly smaller than at one week (fig.   ) but the other relations show small change.

Fig.56 Six weeks specimen. The colon now occupies the right half of the abdomen. The abomasum is full and note its tubular form. As will be seen the rumen extends well over the midline ventrally: only a small amount of liver is visible.

and strong peristalsis of the pyloric antrum (=pars pylorica?)

Observations.

Since the abomasum is not only most easily studied in the smaller subjects but as its activities are also most pronounced in animals a few weeks old it will be most convenient to commence with a description of abomasal behaviour at this age. Later the account will be extended to include a description of the behaviour in both younger and older subjects. In kids a few weeks old the abomasum functions in a manner similar to that of the simple stomach of the dog or other carnivore and if the interval between successive feeds is prolonged for more than a few hours the organ may become quite empty. It is doubtful how often this state would arise in nature where the kids have free access to their dams but in the circumstances prevailing under our system of maintenance it was of common occurrence and the empty organ forms an appropriate point of departure for the description of the activities of this structure.

The empty abomasum contracts to very small bulk and occupies a location immediately behind the diaphragm. Usually a little gas remains in the fundus (fig. 16) and betrays the position of this part but if the fast is extended excessively even this disap-

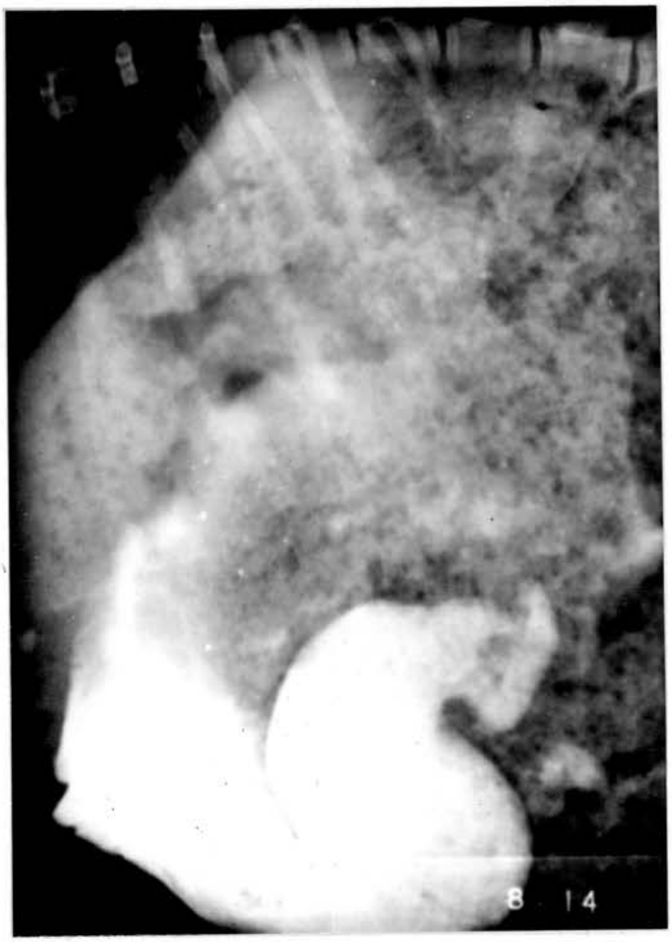


Fig. 57 Subject aged 10 weeks, five hours after feeding.

The abomasum lies almost transversely across the abdomen. Note the sinuous pars pylorica and the anterior flattening against the reticulum. It was estimated that one-third of the meal now lay in the small intestine but the large bowel still seemed to be clear.

pears and the organ becomes quite invisible in plain films. It is instructive to watch the entrance of an opaque meal at such a time. The passage of milk through the oesophagus has already been described: gouts pass through the oesophageal groove and omasum and collect in the abomasum where they form a mass of irregular outline lying below the omaso-abomasal orifice (fig. 59). As this pool increases and the abomasum enlarges, the shadow spreads forwards, downwards and, especially, backwards but without the later form of the abomasum becoming apparent as yet. The caudal extension of the abomasum results in a pull upon the omasum and this, together with the oesophageal groove lying above, changes its orientation, becoming vertically and later caudally disposed in place of the initial cranial inclination. If the meal is of normal size it is only towards its close that the shape of the abomasum becomes clear and it is often some time after its completion before the pyloric part is distinguishable. Moreover, when this part does make its appearance it may be in unfamiliar form, perhaps continuing the main shadow backwards and only later assuming its position dorsal or lateral to the body and extending cranially to give origin to the duodenum.

When the milk first invades the pyloric region a small quantity may escape into the duodenum and

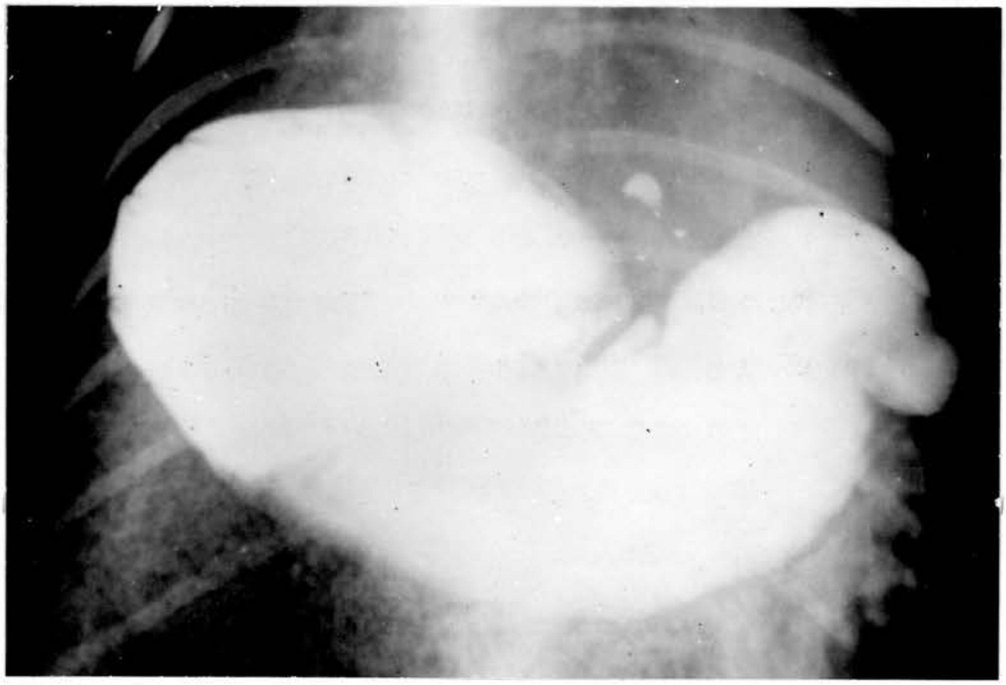


Fig.58 Transverse position of abomasum at age of eleven weeks (not the same animal as in the preceding figure). Observe the contact with each body wall and the indentation on the left extremity due to the abomasal plicae.

The general resemblance to the stomach of the dog is most striking.

The blob of barium before the incisura angularis may well lie in the omasum.

rapidly pass through the first half of the small bowel. This is not normally followed by succeeding fractions of the feed for quite some time.

The ingestion of milk, whether from a bottle, open container or from the udder of the dam is inevitably accompanied by the swallowing of considerable quantities of air, most of which is trapped in the abomasal fundus. This, and the low degree of muscle tone prevailing at this time, gives the organ a sac-like appearance and while this persists there will be little activity and that of low intensity. The gas is however soon reduced in quantity, the greater part escaping in a series of bubbles into the rumen where it again collects until it is finally dispersed. Most of the passage of air occurs during a well defined phase of the ruminoreticular cycle, as may be confirmed on the fluorescent screen for even when the organs are otherwise invisible the movement of the air discloses their activities (fig. 60). It has already been noted that during reticular contraction the abomasal fundus move forwards and downwards: once the bubble (and therefore the fundus) has reached its most anterior position it elongates dorsally and then when it is about to return to its former position there suddenly appears a narrow extension of gas which runs upwards and backwards before it is detached when it rises to join the outline of the ruminal bubble. Whether this movement of gas is limited in occurrence

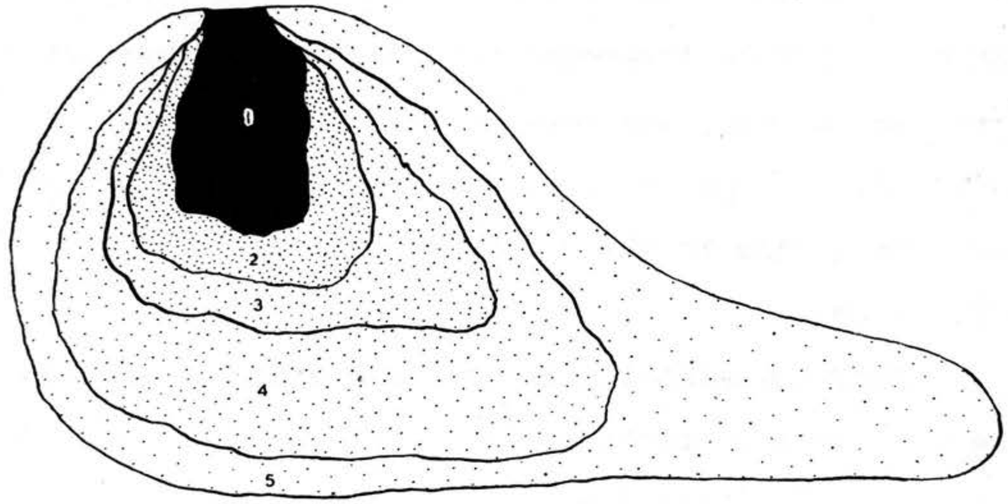


Fig.59 Successive stages in the filling of the abomasum. There is no question of the food first passing along the lesser curvature - the 'Magenstrasse' - as in the single stomach.

by the displacement of the connexion between the omasum and abomasum or by an intermittent relaxation of a sphincter guarding the omaso-abomasal orifice cannot as yet be determined although the former interpretation appears the more probable. Certainly there is little passage of air at other times even in the very young kids in which enormous volumes of gas are often seen.

After the ejection of the excess of gas in this way the abomasum settles down to the more contracted form that is indicative of an increase in the intrinsic muscular tone, and until this change is accomplished there is a period of almost complete inactivity which persists moreover for some 10 or 15 minutes after feeding.

The onset of peristalsis is gradual. On their first appearance the peristaltic waves take the form of shallow indentations, originating at the junction of the corpus and pars pylorica and thence travelling leisurely towards the pylorus and evident only upon the greater curvature of the abomasum: these contractions interrupt the lumen to a very slight extent and many fade out without reaching their destination. Within a few minutes there is a great intensification of activity and whereas the early waves were irregular in their occurrence a regular and rhythmic succession quickly develops: unlike their predecessors

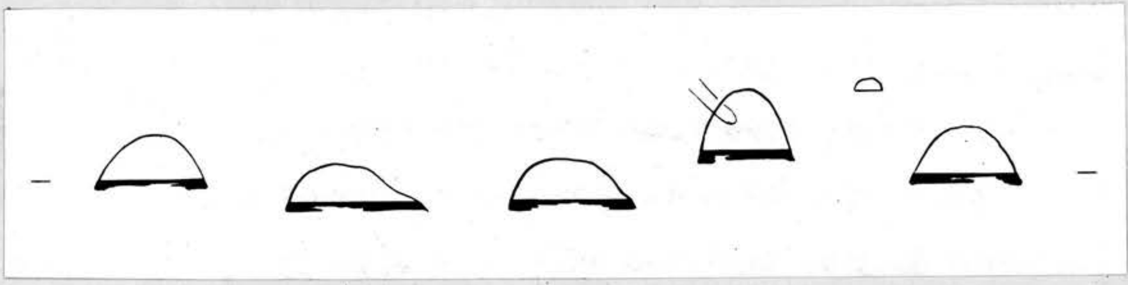
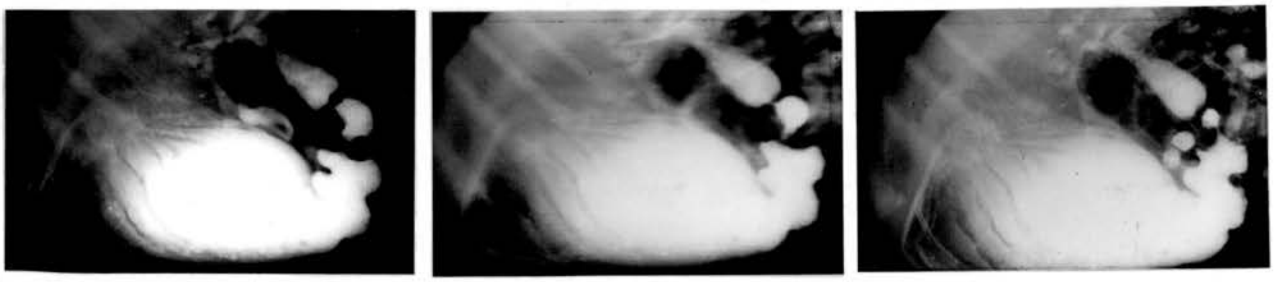


Fig. 60 The movement of the abomasal gas bubble or 'magenblase' during reticular contraction with its subsequent return to its former location.
See. description in text.

which were confined to one margin of the organ these later contractions encircle its girth although they remain more prominent upon the one side, that of the greater curvature (fig. 54). Other changes may be noted: the waves of contraction now arise more proximally upon the body and while still wide and shallow at their origin when they reach the sinus they undergo a striking alteration in appearance, becoming narrower and much deeper, and also much more closely spaced together - the last being an indication of a reduction in the rate at which they travel. They appear to enjoy a further increase in force as they approach the pylorus, widening once more and also becoming much deeper, in many cases almost interrupting the lumen though never actually succeeding in doing so. Most of the early waves passed without interruption to the pylorus but many of the later contractions undergo a characteristic transformation before this point is reached and appear to terminate at a preantral level where they form a deep constriction - the sphincter antri (figures 61 & 62, plate 6). The part lying distal to this ring of contraction then demonstrates a characteristic and rather different motility. In no case is the activity of the abomasum continued into the duodenum.

Considering first however only those waves that continue to the pylorus it has been observed that



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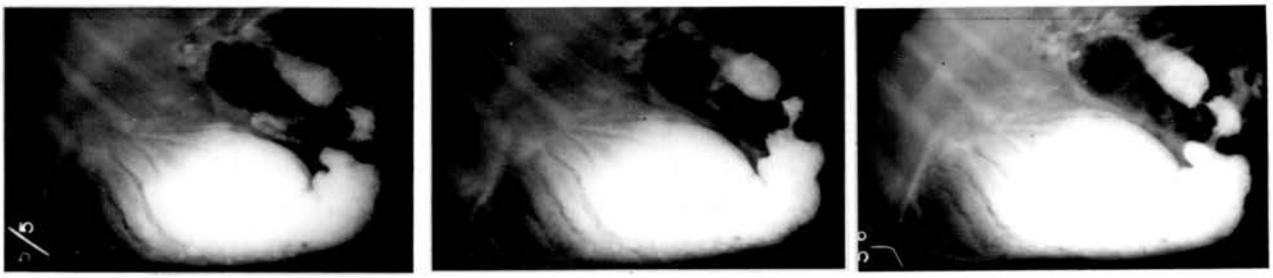

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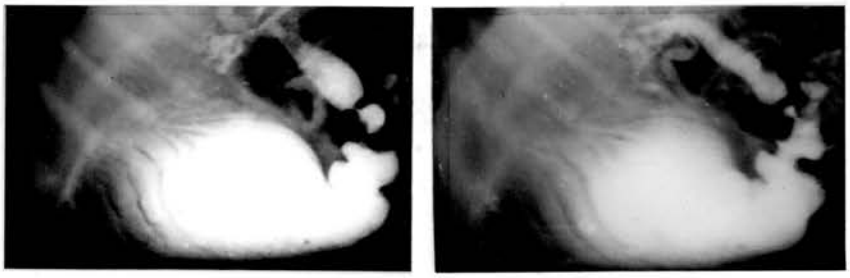

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Fig. 61 Peristalsis and antral systole.

Subject aged 32 days, frame interval three seconds. This extract shows the movement of the peristaltic contractions and the formation of a succession of 'antra' which pass distally to extinction. The pylorus is partly open in certain frames and it is evident that there is some passage of ingesta into the duodenal bulb - compare frames six and eight: on the other hand the connexion between the antrum and the sinus is never obliterated and undoubtedly the greater part of the antral contents remain in the stomach. The last frame shows the beginnings of the bulber contraction simultaneous with the last phase of antral systole and after closure of the pylorus.

these are by no means always associated with an opening of this passage: this in fact is a rather rare event and many complete bursts of activity are completed without its occurrence and therefore without the egress of food from the abomasum (fig. 63, plate 7). Moreover when the pylorus is in fact open it by no means follows that there is a discharge of abomasal contents into the duodenum with the arrival of each wave of contraction. There are of course times when the peristaltic waves are associated with abomasal emptying and then it seems as though the arrival of every fourth or fifth contraction is effective in pushing the food into the bulb. It is tempting therefore to speak of successful and of frustrated waves but the easy acceptance of the peristaltic wave as the actual propulsive factor must be resisted. The point is re-examined later.

The waves which appeared to finish their course at the preantral level are in the majority in the younger animals. It has been said that these contractions terminate at a deep constriction and the appearance of this has been used to divide the pyloric region of the abomasum into two functionally distinct cavities. It must be noted however that this division does not fall at exactly the same level on each occasion which suggests that while there is a functional sphincter antri there is no morphological differentiation of any special muscular ring. Typically the antrum so demarcated contracts as a single unit and the gradual obliteration of its cavity may be termed an antral systole, the subsequent relaxation, when it can be recognised, an antral diastole. In systole it appears as if there is a progressive contraction of all the fibres of the antral muscle which thus bring about a reduction of the antral lumen and, when carried to completion, an obliteration of the cavity. In practice the nature of the cycle is subject to considerable variation much depending upon the degree of closure of the antral sphincter. When this wholly separates the antral lumen from the major segment of the stomach there is necessarily an evacuation of the antral contents into the duodenal bulb through the simultaneously relaxed pyloric sphincter. Much more commonly however the closure of the more proximal sphincter is incomplete and the resulting communication permits a reflux of the ingesta into the proximal part of the stomach. At times both sphincters are relaxed and then it may be a matter of some difficulty to determine the fate of the antral contents which can be expelled in both directions and in variable proportions at the same time. There occasionally follows a phase of relaxation before the arrival of the next wave and the distal part of the stomach refills, with rare exceptions drawing its content from the more proximal region and not from the duodenal bulb (fig. 64, plate 8). More usually as each antrum is extinguished the arrival of the next wave results in the development of a new 'antrum', identical with its predecessor, which in turn moves towards the pylorus and becomes extinct.

In other species in which antral systole occurs it is customary to speak of a concentric contraction of the antrum and the appearance of a gradually diminishing circular outline of this part is described (e.g. Groedel, 1925). In the goat the situation is somewhat complicated by the presence of the torus pyloricus at this level (figs. 45 and 64, plate 8). The torus forms a relatively solid projection from the lesser curvature into the lumen and is itself inactive though to some extent deformable. It forms a firm point d'appui for the contracting fibres and in consequence the cavity assumes an elongated form as the walls and greater curvature are drawn against this immobile mass. The process is described at greater length in the analyses of plates 6 and 7, which should be consulted at this stage.

In addition to the simple peristalsis and the combination of this with antral systole there is also a further variety of activity in which antral systole occurs alone or at least greatly predominates with only occasional and weak peristaltic waves being visible which have no demonstrable relationship to the movements of the antrum (fig. 65, plate 9). But as with other aspects of gastrointestinal mechanics there is almost endless scope for variation and a great wealth of forms exist, many appearing as gradations between other more clearly established patterns of behaviour. Thus, while it is convenient to emphasise a clear cut distinction between the appearance presented when peristaltic waves traverse the antrum from that manifested during antral systole there are many occasions when it is difficult, perhaps impossible, to assign a variety of movement to either category. Some indication of the various configurations and sequences observed may be gained from the study of plates but these by no means cover the full range of appearances (Figs. 61, and 62-66, plates 6-10).

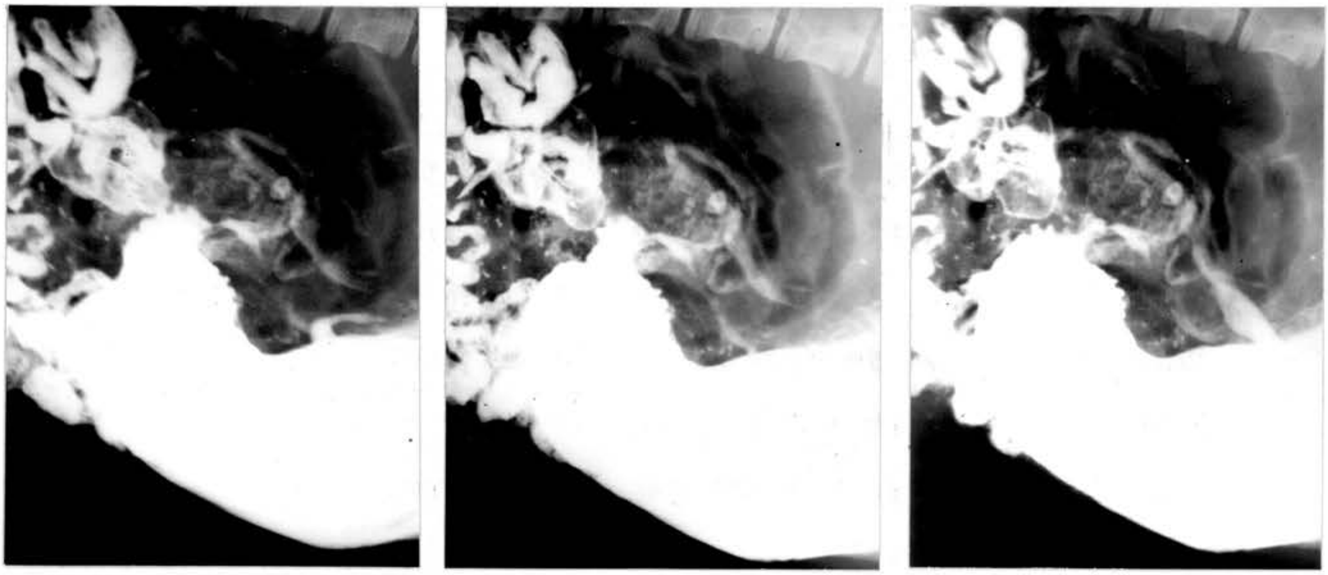
The duration of abomasal activity is another matter characterised by great irregularity for it must be stressed that the movements of this organ are by no means continuous once initiated. Indeed the reverse is quite definitely the case and spasmodic bursts of activity of variable duration alternate with periods of relative or complete quiescience. Under natural conditions the organ does not empty between feeds and the relationship of these bouts of activity to emptying of the stomach would be difficult to determine but in the artificial conditions of our experiments it was possible to study the question more exactly. Commencing shortly after sucking there are relatively frequent alternations of activity and lethargy of relatively short duration but after one or two hours a more prolonged period supervenes during which activity is almost continuous and this persists until the greater fraction of the feed is evacuated. There then ensue increasingly long periods of repose separated by relatively short spells of energectic movement which become less and less effective in ejecting the remaining fraction of the meal: complete evacuation is not likely to take place for upwards of eight hours. (Czepa & Stigler say three hours is sufficient but this is not our experience). The administration of a second feed at any time results in the total suspension of activity and if the additional feed is of reasonable bulk the whole process commences afresh, it being no longer possible to make any useful reference to the fate of the meal first ingested. If the animal is screened during the administration of this second meal it is found that its actual consumption is not necessary for the cessation of activity - the sight of the feeding bottle or indeed any other stimulus which the animal associates with feeding is sufficient for discontinuation of whatever movement was previously in progress. Janes (1958) quotes a number of similar reports of central inhibition of gastric activity in the dog.

The last point indicates the existence of a psychic control of the digestive processes and following upon this it will be convenient to consider certain other evidence which demonstrates the existence of an emotional influence on gastric behaviour. It has alrady been stressed that great effort was taken to avoid disturbing or frightening the animals but it will readily be appreciated that there were many occasions upon which they resented the necessary handling and restraint. At these times the behaviour of the organs was much altered, activity being greatly reduced and often ceasing entirely; the sudden change was so characteristic that during the screening examinations it was often possible to anticipate a struggle from the alteration in the form and behaviour of the stomach. The contemplation of an effort at escape was in itself sufficient to alter the abomasal mechanics a good half minute before any other evidence of the goat's intention became apparent. At these times the first change that was recognised was the stopping of peristaltic and systolic movements and this was shortly followed by a contraction and bunching of the stomach to a more globular form which sometimes persisted and sometimes relaxed to a flaccid state.

The influence of direct palpation or massage of the abomasum, or of the abdomen generally, was less constant. In children (Smith, 1951) palpation of the quiescent stomach will often stimulate activity but in the goat it was more likely to produce a slowing or cessation of movement. In general the result appeared to depend upon the prior state of the organ - when inert it was often, but by no means always, stimulated, when active it was usually inhibited and when lethargic sometimes affected in the one way, sometimes in the other but so irregularly that the response could not be anticipated.

The phenomena described so far have been very readily visible but they by no means exhaust the account of the muscular activities of the abomasum, for the effect of variations in tonicity of the abomasal muscle have as yet received little attention. In the initial stages of digestion the shape of the stomach depends largely upon the intrinsic tone of the muscular wall and the organ in consequence may assume any of a wide variety of forms, the normal range having been shown in the line drawings. It has already been pointed out that activity is generally associated with a moderate, more rarely with a very pronounced, degree of muscle tonicity. Small changes in the muscle tone which may have far reaching effects are unfortunately almost impossible to recognise for a considerable increase in intra-abomasal pressure may be brought about by an increase in tone insufficient to produce much visible change in the appearance of the organ. A slight decrease in the size of the gas bubble might be noted were the conditions suited to exact measurement of its dimensions but the other and relatively incompressible contents certainly exhibit no demonstrable alteration and it is thus impossible on inspection of a single film to determine whether any rhythmic or irregular changes in tone occur. More extended examinations however provide indirect though solid grounds for the belief that such do in fact take place. The lack of any close correlation between the intensity of peristaltic activity and the rate of abomasal emptying has been remarked and often enough the most energetic and superficially impressive states of activity do not result in great movement of the ingesta even though the pylorus is visible in relaxed form. At other times there is a relatively rapid progress of the food when activity is minimal and there appears to be no other explanation of this than the assumption that a differential is created between the intra-luminal pressures of the abomasum and duodenum favouring the onward flow of the food.

In addition to the activity of the main muscle of the abomasum there must be also considered the thin layer of muscularis mucosae to which so much importance has been attached by many who have studied the functioning of the human stomach and bowel. (e.g. Forssell, 1923, 1937: Grettve, 1936). At various times mixing and even propulsive functions (e.g.Cole, 1928) have been ascribed to this formation and some have even suggested that the indentations visible in radiographs and identified as the peristaltic contractions do in fact represent activity of the muscularis mucosae and not of the muscularis propria. The recent very elegant experiments of Pryde and Pendergrass (1954), who combined pneumoperitoneum with the contrast meal, would appear to dispose of this contention. Forssell (1937) also believed that this muscle moulded the mucosa around the larger particles of ingesta which were exposed in this way to the action of the undiluted gastric secretion. Evidence of similar activities in the abomasum of the goat was therefore sought and in the first place the possibility was borne in mind that the muscularis mucosae, which extends into the abomasal plicae, could effect autonomous movement of these folds. Although careful study of these structures was made during the screening examinations and a detailed scrutiny of the serial exposures was undertaken no indication of any such activity was received and it is believed that this possibility can be excluded. Elsewhere in the abomasum the effect of contraction of this layer would be less easily recognised for it must constantly be borne in mind that the image presented of the abomasum, as of the other organs, corresponds merely to the outline of the interior and



1 2 3

Fig.67 Antral systole.

Subject aged nine days, four hours after feeding. Frame interval - probably two seconds.

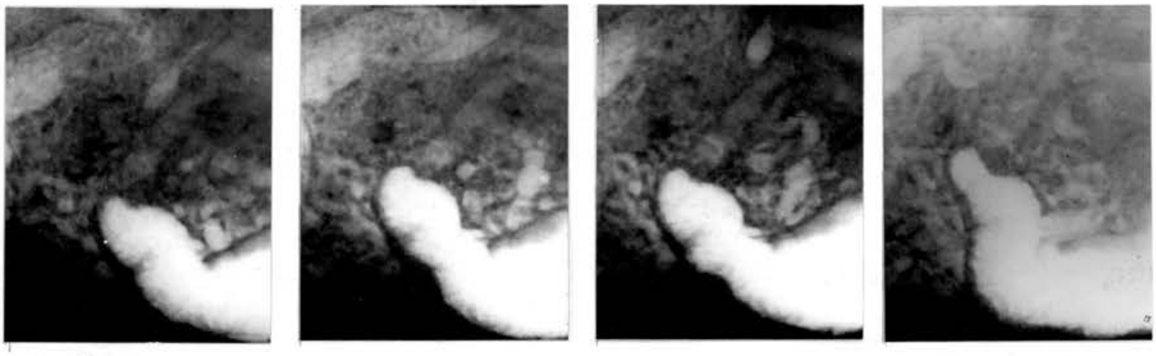
These radiographs show antral systole in the absence of peristalsis. The small irregular indentations of the antrum and sinus are believed to be caused by the activities of the muscularis mucosae. It will be noted that those on the lesser curvature of the sinus are stationary throughout the period covered by the extract.

There is no passage into the duodenum which is very sparsely filled. A considerable quantity of the meal has however passed from the stomach and the caecum and proximal colon, which are not shown, were well filled.

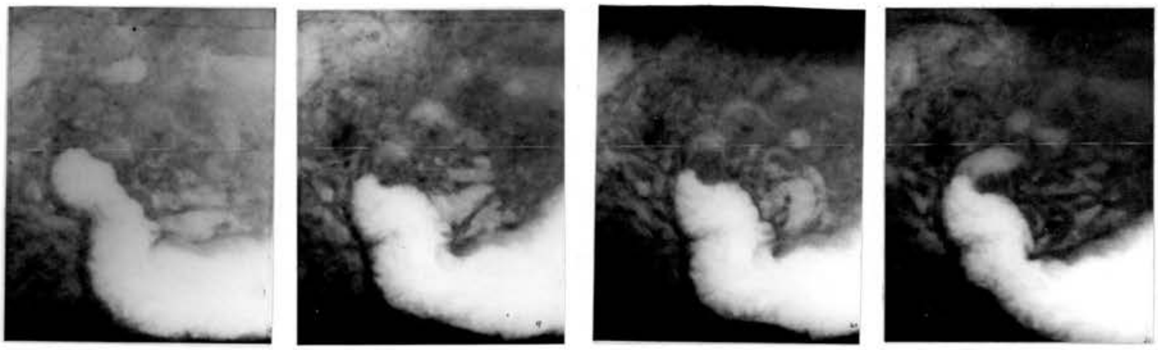
supplies no direct evidence of which layer of the wall causes the interruptions of contour. None the less the characteristic and major indentation of the peristaltic waves obviously exceed in amplitude and force anything that could be produced by the contractions of the weak muscularis mucosae - a decision more confidently reached in view of the demonstration of Pryde & Pendergrass just noted. On the other hand there are often to be seen small but sharply defined indentations of the outlines of the pyloric portion particularly of the distal section or antrum. These features are well seen for example in the series shown in figures67 and 70 and also in many others and exactly resemble what one would expect to see if the mucosa were thrown up in a series of low ridges. Assuming the correctness of this interpretation it is less easy to determine whether such a heaping up of the mucosa is in fact caused by the active participation of its own special muscle layer or whether it is merely the passive effect of the contraction of the main layers with a resulting local superfluity of the covering mucosa. Similar appearances in the fundic region were the subject of previous comment. There seems however to be no question of these folds having an importance in the mixing of the food nor of the muscularis mucosae significantly reinforcing the propulsive activities of the principal muscle layers.

It is also necessary to consider briefly the possibility of a reversal in the direction of the abomasal movements. Apparently a reverse flow of the peristaltic contractions is at times witnessed in man and Trautman & Schmitt (1933) and Akessenowa (1932) report a regular filling of the rumen and reticulum from the abomasum in the kids they studied. No such observation was made during the course of the present enquiry. On a very few occasions the rumen of a young bottle-fed kid was discovered to contain milk shortly after feeding but while this could conceivably have been brought upon in this manner the alternative interpretation that the oesophageal groove reflex was for some undetermined reason not entirely effective seems preferable for on no occasion during the many screening sessions was any activity seen that could have facilitated a reflux from the abomasum.

So much for this group aged two to four weeks. In the immediately neonatal period the abomasum is comparatively inactive, and show long periods of inertia which are broken by shorter spells of relatively gentle activity. This is often long delayed in onset and consists when it appears of weak and broad waves of contraction which pass over the entire organ and not only do not give way to systolic contraction of the antrum but commonly fail even to deepen or intensify over the pars pylorica. Several hours may elapse before even the smallest trace of the feed appears in the gut and the complete evacuation of the stomach may require upwards of sixteen hours during the first few days of postnatal life. The period of indolence is however short lived and by the time the animal is a week old very significant increases in activity are always evident. Already there is a much more vigorous type of peristalsis, particularly over the more distal part of the organ and antral systoles begin to make their appearance. The onward movement of the food is greatly hastened with these developments. These changes continue and the full range of activity is normally established by the end of the second, or at the latest, third week of extra-uterine life. Then follows the period, already described, when the movements are most intense and while it is impossible to put a precise limit upon the duration of this phase, or to notice a day to day alteration in the force of the contractions, some diminution of the vigour and amplitude of the movements can usually be discerned before the completion of the first six weeks. At first this change consists of diminished frequency of the very powerful contractions and the intensity of the more common movements is unimpaired but later these too are affected and a general slackening of activity is clearly recognisable. This decline in activity follows upon the change in the composition of the diet for now the kids no longer subsist exclusively upon milk but rely more and more upon the solid fodder for their sustenance. There is thus a fundamental change in the physiology of the abomasum. The discharge of the more fluid contents of the forechambers although by no means continuous is never long interrupted and the volume of ingesta remaining in the abomasum is continually augmented by small quantities entering from the omasum. Observation on animals to which an opaque meal has been given by stomach tube often show the passage of some of the contrast agent into the abomasum within a very few minutes of its administration and although on other occasions there is a more extended period before any of this medium can be detected in the abomasum this is rarely more than sixty minutes in duration and never for so long as two hours. In consequence the abomasum never approaches an empty or contracted state and its filling depends to an ever decreasing degree upon the administration each day of the few milk feeds. None the less for so long a time as the administration of milk is continued it will be found that its entrance into the abomasum results in a complete though temporary inhibition of the motor activities of this organ.



14-17



18-21

Fig. 68 Abomasal activity in an older animal.
Subject aged 3 months, 5 hours after feeding.
Frame interval $1\frac{1}{2}$-$1\frac{3}{4}$ seconds.

The movements of the abomasum are confined to the pars pylorica which is extended and narrow. The passage of the peristaltic waves which are more evident on the greater curvature and the indentation of the torus pyloricus combine to give an appearance of sinuosity. On the fluorescent screen the shape and sluggish activity produced a 'writhing' effect. It will be noted that the milk shadow is flocculent.

At the same time, and for the same reason, the discharge of the contents of the abomasum loses much of its earlier spasmodic nature and continues in much smaller bursts throughout the day - and presumably in the same way through the night hours also. The change in feeding habits is associated with a change in the appearance the organ presents when active. In the first place it is found that frank and clearcut antral systoles become increasingly rare and perhaps entirely disappear by the tenth week. The peristaltic waves also lose much of their vigour and rarely interrupt the line of the organ to a marked degree. Rather they appear as shallow but wide zones of contraction which pursue a more gentle course over the organ but which take a rather unusual form as they reach the pyloric part. The appearance is difficult to define but is quite evident in certain of the illustrations (figs. 68 and 69, plate 11) and depends in some measure upon the assumption by the abomasum as a whole, and by the pyloric part in particular, of a more contracted and tubular configuration, a process that continues for some time after this age until the final adult form is acquired. The resulting impression is of sinuosity in outline of this part which, on the fluorescent screen, appears to undergo slow writhing contractions most characteristic when seen but extraordinarily difficult to describe. In part the indentation of the outline produced by the torus pyloricus is responsible since it gives an asymmetrical effect to the most distal part of the organ which is reinforced by the tapering form of the more proximal section and by the formation of a series of ill-defined ampullae which progress in regular succession towards the duodenum.

In yet older kids - those aged three months and upwards - there is nothing that distinguishes the mechanics of the organ from its behaviour in the adult animal. Here the movements are largely confined to the pars pylorica and the corpus abomasi is rarely affected by the passage of the peristaltic waves. On the pyloric part the waves resemble those just described and while they frequently appear to be pronounced following each reticular contraction they are neither a constant sequel to this nor entirely absent at other times. In the older animals one not infrequent change that is most striking is the fixing of the position and amplitude of the waves and this may persist at times for quite lengthy periods giving what may perhaps be described as a 'frozen' appearance. This state is not recognisable in a single film for here the waves appear in motion but it is of course very obvious in a series or upon the screen.

Before leaving the description of this chamber of the stomach some references must be made to the character of the shadow produced by a milk meal. On first administration this appears as a homogeneous fluid of good density. After a period varying with the age of the animal, the previous contents of the abomasum and probably also with other factors which are not susceptible to analysis by radiological means, it loses its original character and forms a more woolly and less even shadow. The coagulation of the milk protein and the later disruption of the coagulum are of course the cause of this effect. This irregular appearance persists for a considerable time and portions of the clot are freely passed into the gut. Somewhat unexpectedly this 'clotting' effect was most striking in animals aged six to ten weeks rather than in the youngest kids (compare figs. 49 & 88a, plate 14). A certain difference in appearance of the clots also distinguishes the animals of the two groups: in the youngest the clot is woolly but continuous in appearance whereas in the animals on mixed diet it tends to break up into well defined particles with hard and distinct outlines. No explanation of these differences is offered.

Discussion.

Previous workers who have described the mechanics of the ruminant stomach have had relatively little to say concerning the movements of the abomasum and the interpretation of the present observations will be better assisted by reference to accounts of the corresponding activities of the stomach of other species. The comparison is facilitated by the general similarity of the radiological appearances and motility of the abomasum and of the simple stomach but this should not be allowed to obscure the fact that the features are analagous and not homologous.

On the whole the results described for different animals are in close agreement and it is notable that individual authors tend to report less difference between the various species they have themselves examined than exists between the accounts of different authors concerned with one and the same animal. One of the principal points on which conflict arises concerns the nature of the antral systole and the determination of its relationship to the simple peristaltic waves that traverse the more proximal part of the organ. At one time a lively controversy centred on this question and while the argument no longer occupies a prominent place in discussions of gastro-intestinal mechanics it was not satisfactorily resolved: it is perhaps for this reason that not a few of the authors of modern textbooks of physiology and radiodiagnostics pass the matter over without comment and without committing themselves to an exact description of the activity of the distal part of the stomach.

One group of workers, following the original observations of Hofmeister & Schutz (1886) contended that the peristaltic wave travelled slowly over the preantral part of the stomach, increasing in intensity as it approached the pylorus and terminating some little way proximal to this point, forming a deep constriction which cut off the distal segment - the antrum pylori: this then underwent systolic contraction. Subscribers to this view included Holzknecht (1906) and Groedel (1909) who produced supporting evidence in the form of serial radiographs. This version of the radiographic appearances was first attacked by Cannon (1898) who described, in the stomach of the cat, the uninterrupted passage of the peristaltic waves to the pylorus. Most later workers, and in particular most radiologists, favour Cannon's interpretation which in its turn was endorsed by the serial radiographs of Kaestle, Rieder and Rosenthal (1910-11). According to the last-named workers the different appearance in the prepyloric region is due to an exaggeration of the peristaltic waves in this region. This view denies the existence of an antrum pylori as an anatomical entity and the following quotation from their account has been given wide currency as indicating the essence of the matter: "As the old antrum disappears a new antrum is developed from the wall of the body of the stomach. This new antrum passes pyloruswards, and ultimately takes exactly the place of the old antrum whilst another new antrum begins to form'. Cole (1911) provided further important support for this school. He classified the types of activity according to the numbers of waves evident at a time and spoke of one-cycle, two-cycle types, etc., and he suggested that the movement described by the opposing group represents merely a special case in which the spacing of the peristaltic waves is such that the 'antrum' is formed and disappears before its successor begins to develop.

Many other reports followed and the question was still open when McCrea, McSwiney, Morrison and Stopford (1924) re-examined the motility of the stomach in man, cat, dog and rabbit combining radiological with direct observations in the laparotomised experimental subject. They found, in all species, a combination of peristalsis with antral systole and, except in the cat, this was the commonest type of movement. Unmodified peristalsis also occurred and they recognised yet a third type in which peristalstic waves continued over the formed antrum. In many examinations they observed active peristalsis at a time when the antrum remained in diastole and they conclude that the two activities may proceed simultaneously with different rhythms. Unfortunately McCrea and his colleagues published no radiographs and the drawings which illustrate their paper do not make clear the distinction between the varieties of activity. This and later reports did little to clarify the situation and Alvarez (1948) seemed to state the commonly held view when, reviewing the subject he concluded that both groups of observers were in some measure correct and that much of the confusion stems from the very variable forms assumed by the active stomach. According to Alvarez the transformation of the peristaltic wave into antral systole results, in most if not in every case, from the contractions of the longitudinal and circular muscle becoming asynchronous as the pylorus is approached.

The recent description of Keet (1957) appears to put the matter on a firmer basis and his interpretation of the prepyloric contractions may be quoted at some length. But in order to comprehend his meaning it is first necessary to refer to certain of the anatomical observations of Torgerson (1942). Torgerson described three localised thickenings of the muscularis propria in the prepyloric region of the human stomach. The first of these surrounds the pyloric orifice on the side of the greater curvature and accounts for the separation of the images of these organs that is apparent in the normal radiograph; the second lies considerably more proximally and surrounds the greater curvature at the entrance to the canalis (approximately equal to the antrum of the present account), while the third lies on the lesser curvature at the convergence of the other thickenings and consists of a muscular torus which completes the division of the stomach and duodenum.

The following extract from Keet gives the gist of his views, but the original account, and in particular the illustrations, should be consulted. "....initially, at the stage when the peristaltic wave ceases to advance, a muscular contraction occurs in the normal division between s tomach and duodenum on the lesser curve. Next this contraction increases and merges with the original stationary peristaltic contraction (at the level of the proximal muscular loop) to form a single, wide area of muscular contraction on the lesser curve. At this stage there are two contracting muscular loops on the greater curve, viz., one in the normal division between the stomach and duodenum and the other some distance orally to this and confluent with the stationary peristaltic wave. The contraction of these two loops results in the formation of a 'loculus' of the gastric lumen on the greater curve. The continued widening of their respective impressions indicates a progressive contraction, which results in the further compression of the 'loculus', causing the latter to become smaller.... At the last step, that of maximal contraction, both loops contract still further thus causing a concentric narrowing ... and its eventual disappearance".

The quotation will recall a number of features noted in the description of the abomasal movements of the kid. Can it be assumed that antral systole in this animal follows the same pattern? Before attempting to answer this question certain features of the muscular anatomy of the region may be noted. Torgerson claims that the same muscular features are present in the abomasum of the ox as in the pre-pyloric region of the human stomach but he admits that they do not appear as swellings in the musculature: Martin-Schauder (1938) and Ackerknecht (1943) do not recognise the existence of separate loops and personal examination of the abomasum of the goat has shown them to be very poorly developed and hardly recognisable as independent formations. The distal, pyloric, sphincter is notably poor in the ruminants and according to Martin-Schauder is best represented in the sheep: Torgerson notes that it partially inserts in the mucous membrane swelling and all agree that the circular fibres in the region of the torus attach to that protuberance.

Referring now once more to the radiological appearance of systole in the kid it will be found that it differs in certain material features from the account furnished by Keet, but the divergencies can be correlated with the special anatomical arrangements. In the first place there is no marked widening of the gap between stomach and gut at the onset of the contraction and even in the terminal stage the increase in width is relatively slight. Secondly, the cavity, or 'loculus' to use Keet's term, tends to become more cylindrical than in man. These distinctions are obviously associated with the weak pyloric sphincter and the anchorage of the circular fibres to the torus: the other details correspond very closely, indeed the two sets of radiographs show a remarkable similarity, and it is impossible to resist the conclusion that Keet's interpretation is equally valid for the two species, and probably for others also.

There is, however, one important point on which the two accounts differ: Keet's observations were made on over three hundred normal subjects and he states that in every case the prepyloric contractions followed a common pattern. This is not only very different from the experience with the goats but also, setting aside all animal experiments, contrary to almost all radiological observations on the human subject. The remark of Torgerson, made incidentally in the course of a discussion of another topic, that 'the total contraction is a comparatively rare form of contraction in man' is not easily reconciled with it, and other authorities could be quoted who, if less extreme, at least do not suggest uniformity of movement in this region.

Uniformity of appearance is certainly not the experience in the kid and the extent of the variation has already been noted and to some extent illustrated. It seems certain that in the kid there is no fundamental distinction to be drawn between the systolic and the peristaltic contractions and that the former owe their origin to a modification of the latter: such an explanation does of course provide a ready explanation of the graded forms that join the extreme, and considered independently, quite dissimilar types of activity and not only accounts for the different appearances in animals of similar age but also for the gradual transformations that are manifested by the individual during its early life. It is not difficult to see how the different activities arise. Peristalsis requires the co-operation and co-ordination of the longitudinal and circular muscle: the former stratum acting alone shortens the segment; the circular fibres constrict the lumen, and there can be endless combinations of these effects with the reactions of the sphincteric loops determining the fate of the stomach contents at this level.

In a short preliminary note Dyce, Merlen & Wadsworth (1953) suggested that the antral systoles were often independent of the peristaltic contractions: more extensive observations and fuller consideration have not confirmed this impression. In the vast majority of cases the birth of each systole coincides with the arrival of a peristaltic wave which appears to 'trigger off' the subsequent activity in the distal part; often however the peristalsis may be poorly defined and may easily escape notice. It is not denied that there are occasions when powerful systoles are evident without any sign of peristalsis but it now seems unlikely that there can be simultaneous and unco-ordinated movements of the two varieties.

The kid, like the human infant, possesses a relatively sluggish alimentary tract during the immediately postnatal period. In the infant it is known that the muscular development of the stomach is subject to great increase after birth but in the kid the onset of powerful contractions of the abomasum is surely too rapid to be accounted for in this way: moreover very powerful (and incidentally systolic) contractions of the pyloric part of the abomasum may be evoked by appropriate stimulation in foetal lambs long before term is reached (Duncan & Phillipson, 1951). The relative inertia of the abomasum of the neonatus represents a physiological rather than an antomical unpreparedness.

On the whole the phase of greatest and most powerful motility coincides with the later part of the period during which the animal lives largely upon milk and the diminution of these activities proceeds apace with the increasing consumption of other foodstuffs. It is obviously necessary to enquire whether the two processes are related and in the first place it may be useful to see what is known of the comparative differences in gastric meachanics of animals of carnivorous, omnivorous and herbivorous constitution. The literature is not very helpful. The paper of McCrea et al. indicated that the gastric activities of man, rabbit, dog and cat were very similar: the frequency with which antral systoles were developed showed some variation but as already pointed out it was the stomach of the last-named animal which showed the greatest departure from the common pattern and not, as would have been expected, the stomach of the herbivorous species. The experience of others has not always been the same. Torgerson, for example, did not observe total contraction of the distal stomach segment in the rabbit even once during extensive observations although he is careful not to exclude the possibility of its occurrence. Kryzwanek (1927a,b,c.) also examined a number of species by radiological methods and although he gives a rather poor account of the gastric movements he found no distinction between the herbivore (guineapig), omnivore (rat) or carnivore (dog). Carlin (1928) and Kästle (1918-9) reported both types of contraction in the dog but Dukes (1955) appears to believe that the peristaltic waves never continue to the pylorus in this animal. Neimeier (1939) examined the stomach of the piglet and described the waves proceeding to the pylorus but personal observations in the same species, as yet unpublished, showed a marked preponderance of systoles though admittedly in rather younger animals. Hill (1952) did not observe systolic contractions in the horse. Henderson's observations (1942) in the newborn infant showed that even at this period both peristaltic and antral contractions occur in the human stomach. These and other results are too indefinite, and in many cases are based on far too few observations, to permit a final conclusion but they are suggestive that there is no close association between the nature of the diet and the type of motility characteristic of the stomach of different species.

Some parallel studies made on the abomasum of the kids reared exclusively upon milk may be more to the point. For the reasons already stated this part of the enquiry was drastically curtailed and results were obtained from only two of these goats and then only for the first three months of life. They have not been reported in full since the observations were so limited in scope and obviously require further confirmation but it may be said that in the animal which survived longest there was no sign of any diminution in the force or modification in the nature of the systolic contraction up to the time when it was destroyed. Tentatively it is suggested that these observations do not support the conclusion reached from a consideration of the comparative literature but on the contrary point to a correlation between the milk diet and the abomasal activity, but whether this is due to the chemical or physical composition of the food or to the intermittent filling of the abomasum must at present remain in doubt. Further investigation of this point is indicated.

It was hoped that this investigation would cast some light upon the function and purpose of the torus pyloricus which also occurs in the pig and in a number of other unrelated species not apparently united by diet or a general similarity in gastric anatomy (Pernkopf & Lehner, 1937). A similar, though impermanent, formation described by Forssell (1937) in the human stomach under the title of prepyloric bar appears to be formed by the raising of a fold of mucous membrane under the influence of the muscularis mucosae: similar folds, though less striking in their development than those illustrated by Forssell, are familiar in the stomach of the dog and horse in the dissection room. The function of such a formation is obscure: Forssell suggests that it acts as a filter retaining the larger pieces of ingesta but this conjecture is hardly convincing and it is not easy to see that the bar would possess any advantage to this end beyond that already provided by the narrow aperture of the pylorus. In studying the antral systole it has occasionally appeared that the torus divides the ingesta into two parts, one passing to either side of its base but while the effect is striking no obvious value attaches to such a duplication of the stream. It has been noted that it forms a firm basis for the attachment of the circular muscle fibres but in most species the same end is served by the development of a muscular knot which does not project into the lumen (Torgerson).

Turning now to the consideration of the evacuation of the stomach, it has been shown that the appearance of the peristaltic contractions is very misleading and that these movements are probably of relatively minor importance in determining the movement of the gastric contents into the duodenum. It is of course true that an advancing ring of constriction will not have a great effect on the propulsion of the contents unless it is complete or at least sufficiently tightly drawn to impede the reflux of food into the proximal segment: but granted this, Alvarez surely goes too far when he denies all propulsive effect to the peristaltic contractions. Probably, however, it is the mixing of the food by these movements which is of greater importance. It is difficult to appreciate this from the radiographs, particularly from the single plate which may give the appearance of great activity without reminding the observer of the slow rate at which the contractions advance.

The systolic contractions of the antrum have a greater significance in the expulsion of the ingesta although even these are less effective than first appearances suggest for they, too, commonly leave open a communication with the body of the stomach which provides an escape route for part, if not all, of the material trapped in the antrum. Undoubtedly much of the propulsive force comes from an increase in the general tone of the proximal part of the abomasum or from systoles of the body. The same appears to be true of the infant stomach (Henderson, 1942; Rogatz, 1924a, b, and others). Unfortunately these activities are almost impossible to study by simple radiological means, particularly when complete immobilisation cannot be obtained: but the existence of the phenomena is sufficiently established. Dukes & Sampson (1937) described alternate contractions and relaxations of the body of the exposed abomasum of the sheep while the importance of the tone of the corpus and fundus of the human organ in forcing the food down into the muscular pars pylorica is a commonplace.

Discussion of the emptying of the stomach also involves consideration of the pylorus and the duodenal bulb and necessarily anticipates somewhat the description of the latter part of the tract. The analysis of the series reproduced in figure 63, plate 7 and the pictures themselves may be referred to as exemplifying the results obtained in this part of the investigation.

The essential feature determining the flow of ingesta into the duodenum is a favourable pressure gradient between the antrum and the duodenal bulb and in the absence of this food will naturally fail to leave the stomach however dilated the pylorus or vigorous the gastric activity (Brody, Werle, Meschan & Quigley, 1940). The sequence of events in this region was well described by Werle, Brody, Ligon, Read & Quigley (1941) who studied antral systole in the dog, recording simultaneously the pressure in the antrum and in the duodenal bulb, the passage of the peristaltic waves, the state of the pylorus and the passage of the contrast meal. According to these workers the pylorus normally remains open and contracts only as the peristaltic wave reaches its level: the pyloric muscle is thus to be regarded as a thickened continuation of the antral muscle and not as an independent sphincter formation. They explain the intermittent passage of antral content as being due to the generally low and ineffective pressure gradient across the pylorus which is suddenly increased with the arrival of the wave of contraction at the more distal part of the antrum. The advancing stimulus reaches the pylorus before the completion of the systole, whereupon contraction of this part ensures that the discharge of food is halted before the increase in intra-bulbar pressure which follows can effect a reflux of the duodenal contents into the abomasum. In consequence of pyloric closure the succeeding contraction of the bulb results in the projection of its contents into the distal part of the duodenum. Werle and his colleagues report that while this account describes the usual sequence variations are common: many waves do not cause evacuation even when the pylorus is open, presumably because of an insufficient difference in pressure between the parts, while occasionally a too rapid development of intra-bulbar pressure anticipates the closure of the pylorus and allows a reverse flow into the stomach.

Comparison of this account with many of the series obtained in the goat showed numerous similarities (once more see the analysis of fig. 63, plate 7). In the kid the duodenum appears to play a rather more passive role than in the dog but the state of the pylorus and its relationship to the various stages in antral contraction appear to be largely the same in both species.

It is now common to speak of the presence of a pacemaker in the gastric wall regulating the development of the peristaltic contractions (see discussions in, for example, Alvarez or James) and in the single stomach this is generally located towards the cardia. In the ruminant the activities of the abomasum are often related to those of the other chambers of the stomach, in particular to the contractions of the omasum and reticulum and the pacemaker can thus be placed outside the abomasum (Brunaud & Dussardier, 1953b). Peristalsis is often described as being initiated after reticular contraction either because of a mechanical tipping of the ingesta into the end of the organ when the fundus is raised (e.g. Phillipson, 1939) or by the spread of the impulse from this pacemaker (Duncan & Phillipson, 1951). The very nature of our method of study prohibits the expression of an opinion on the existence of such a differentiation and it must be stated that the relationship of reticular contractions to abomasal peristalsis was never very clear and while the mechanical condition would necessarily be different in the recumbent animal, the lack of correlation between the contractions of the forechambers and those of the abomasum was almost as evident in those examined when standing erect.

Before leaving the subject it may be appropriate to refer to the vigour of the activities manifested by the abomasum of certain of our kids in distinction to the relative quiescience stressed by Magee (1932) and others. This presumably may be ascribed to the immaturity of these subjects and serves to emphasise the importance that attaches to taking cognisance of the age of the animals in any experiment involving the alimentary tract.

Fig.70 Subject aged $2\frac{1}{2}$ weeks, 2 hours after feeding. The abomasum is active and weak indentation of the corpus is visible in addition to more vigorous movements of the pars pylorica. Note also the abomasal plicae. The pylorus appears open and the duodenal bulb unusually wide. It is probable that the flecks of barium near the spine represent the dorsal limb of the duodenal loop.

Weak and irregular shadows occupy the first part of the free small intestine and lie centrally in the abdomen and above the abomasum. A more continuous strip of small intestine lying on the floor of the abdomen to the rear of the abomasum represents the intermediate part of the small intestine and this shows some segmental activity. The distal section is well filled and the coils are both wide and of a considerable density. These also show segmentation patterns.

The Duodenum

Radiological Anatomy

General considerations.

The first part of the duodenum of the goat is expanded and forms a duodenal bulb (figs. 43, 70, 88c, plate 14, etc.), similar to that occurring in man but this soon tapers to the relatively narrow calibre of succeeding parts of the small intestine. In the older animals the origin and succeeding part of the duodenum lie under cover of the ribs, between the liver and the rumen, and ascend almost vertically behind the greater curvature of the omasum to the region of the hepatic porta; here the duodenum undergoes a series of close bends which together form the portal flexure (fig. 43): the portion which emerges from this convolution describes a horizontal U-shaped loop which carries it first towards the pelvis and then, turning dorsally at the level of the fourth or fifth lumbar vertebra, forward once more to the region of the right kidney whence it descends to continue into the mesentery as the jejunum (fig. 71).

It is rare for the entire length of the duodenum to be visible at once and as with certain other organs a composite impression of its anatomy must be built up from the examination of several plates. As a rule the bulb remains well filled during the period of active discharge of the abomasal contents but the

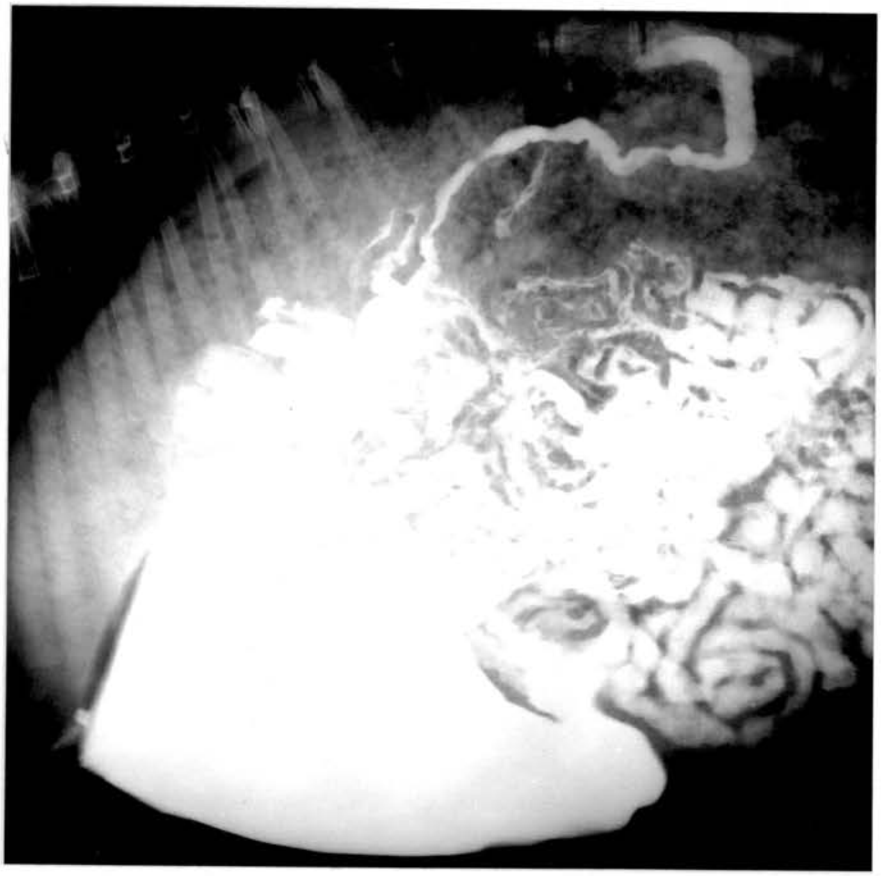


Fig. 71 Subject aged five weeks, two hours after feeding. The omasum is distinct. The bulk of the meal remains in the abomasum which shows peristalsis of body and pyloric portion. The duodenum is visible in its terminal part and is seen running ventrally to join the jejunum: the pelvic flexus is unusually distinct. The contours of this part of the intestine are much affected by activity and show the abrupt junction of regions of very different calibre.

The first part of the small intestine is very irregular in outline and in the arrangement of its contents. More posteriorly it is better filled and is marked by segmental indentations. Many largely collapsed coils are visible below the duodenum and these are marked by longitudinal striations.

passage of food through the remainder of this organ is both intermittent and rapid. The radiographic appearance reflect this functional distinction for while the bulb is usually clearly visible the distal portions are largely collapsed and if discernible at all then marked by a series of irregular streaks (fig. 63, plate 7).

The appearance of the bulb merits closer inspection (e.g. figs. 43, 63, 70, 73 & 47). Its width and form vary considerably and while sometimes it is distinctly delimited by a rapid loss of calibre at other times it tapers so gradually that it is difficult to define its extent. A terminal sphincter is rarely suggested. Examination of the fresh specimen shows that it is especially thin walled and as its intrinsic tone is often low its form varies considerably when it is compressed by the surrounding organs. When well filled and tense it has a regular outline and a density in keeping with its dimensions. Very often however it is only partially distended and then it may be of uncertain outline and of low density the latter feature indicating its distorted shape on section (fig. 66, plate 10). The low opacity is often very obvious and is recognised when the relative densities of the antral and bulbar shadows are compared. On the other hand it must be admitted that the dorsal view does not always demonstrate the partial collapse

Fig.72 Dissection of kid aged eleven days. The duodenum may be followed arising at the pylorus and ascending to the portal flexus before running caudally to its pelvic bend: beyond this it is concealed by the right kidney. Note also the omasum and the disposition of the intestines.

The course of the duodenum may be identified in the radiographs reproduced on figure

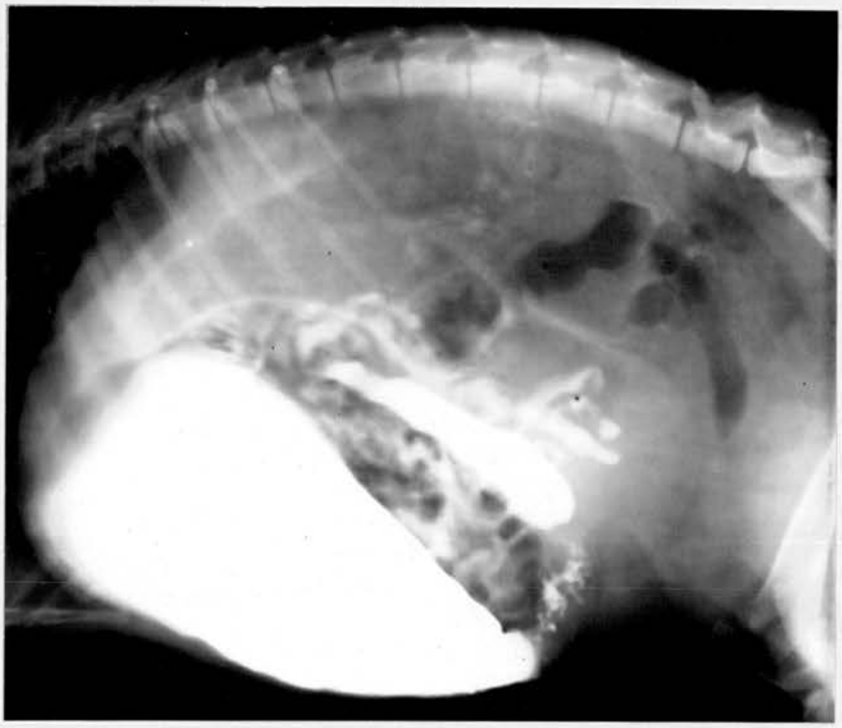


Fig.73 This film shows a rather long and poorly differentiated duodenal bulb. The pars pylorica is almost empty but contains sufficient contrast agent to show its position and to hint at the existence of mucosal rugae. The animal was lain upon its side and the abomasum is distorted.

Other views of the duodenal bulb are provided by figures and lateral compression that are assumed here (fig. 88c, plate 14). Occasionally the shadow is uneven and then commonly it is denser along one or other border, indicating that the cross section of its lumen must resemble a keyhole in outline (fig. 75, plate 12). Apart from these factors the shadow tends to be uniform and irregularities reflect the heterogenous condition of the content and not a mucosal pattern such as is described in man. There is in fact no sign of mucous membrane folds and presumably no autonomous activity of the mucosa - a species distinction undoubtedly associated with the poor development of the muscularis mucosae in the ruminant (Trautmann, 1907).

Although the distal stretches of the duodenum appear to be of irregular width this is due to the irregular filling and localised activities of the part and not to any permanent variations in calibre (figs. 71, 76, etc.). The streaks that are visible are usually about 2-4 inches in length and normally taper to each extremity.

Postnatal development.

In the youngest animals the first part of the duodenum runs forward from the caudally placed pylorus before it ascends to the porta and thus it comes to lie dorsal to, or to one side of, the corpus: if laterally placed it commonly lies on the right. Its course is thus clearly divided into horizontal and vertical sections and it is rare for the bowel to follow the direct line to the portal flexure (fig.72). As the animal ages the abomasum is gradually withdrawn to the more anterior part of the abdomen with a consequent, and readily appreciated, alteration in duodenal topography for as the pylorus comes to lie more cranially it permits a more direct ascent of the relatively shorter first part of the duodenum.

In older animals it is difficult to study the more distal part of the organ but changes in this section are small although temporary deviations occur which are due to the varying distension of the gastric chambers. The important relationships to the liver and omasum are constant.

Duodenal motility.

Previous literature.

Relatively little is reported of the movements of the duodenum in the ruminant. Czepa & Stigler confined their remarks to noting the distinction between the appearance of the bulb, which they found generally filled, and the remaining, usually empty, portion of this part of the intestine. Hagemeier (1937) in a later radiological study of the ruminant intestine gave a rather fuller account. He described a collection of the ingesta in the bulb and the periodic division of this by a transverse constriction across the widest part: the more distal portion was then rapidly passed into the succeeding part of the duodenum by a peristaltic rush which faded at the extremity of the bulb. In its further progress the ingesta appeared as a tapering column of some 3 inches length which was passed exceptionally rapidly through the bowel by a form of activity which provided no evidence of its nature. The part that was left behind remained immobile and was added to by successive bursts of abomasal activity. Apparently division sometimes occurred but was followed by no movement and the divided portions later rejoined.

Dukes & Sampson (1937) examined the duodenum in the open abdomen and described small wavelets running over the outer surface. They distinguished these from the peristaltic rushes evident on the more distal parts of the intestines. It will be recalled however that the methods adopted by these workers are open to some criticism. Dyce, Merlen & Wadsworth (1953) considered that the duodenal movements resembled those occurring in the dog, an observation that now appears most misleading, at least in so far as the initial section of the duodenum is concerned.

Observations.

The movements of the duodenum are extraordinarily diverse. As a rule a fundamental distinction may be made between those activities which involve the duodenal bulb and those which are confined to the more distal part of the organ and which have a greater resemblance to the activities of the remainder of the small intestine. But even this division is not absolute and there are occasions, admittedly comparatively rare, when the entire duodenum seems to be involved in a uniform pattern of behaviour (e.g. fig. 75, plate 12).

The entrance of the ingesta into the duodenum is largely controlled by the behaviour of the abomasum and the patency of the pyloric opening: the role of the duodenum is mainly passive and the bulb distends to receive each new portion of the ingesta. Its manner of doing so has already been remarked and its filling is more readily recognised by the increase in density than by the expansion of its transverse dimensions. If however the process continues without any active movement on the part of the duodenal muscle the bulbar contents overflow and pass some way into the duodenum proper: on occasion they may extend to the portal flexure or even beyond this landmark into the horizontal loop. In these rather unusual circumstances this part of the intestine becomes filled by a continuous column of ingesta. This passive overflowing is commonest when the distal part of the free small bowel is filled for this state appears to exert an inhibiting influence on the duodenal movements.

More usually however long before this stage is reached the duodenal bulb reacts in one of a number of ways, for its motility follows no single pattern. The alternative movements appear to have no connexion with the age of the animal or with the food it receives and it will be unnecessary to consider either of these factors. It has already been noted that in the older kids the emission of abomasal content is rarely suspended for longer than ten or fifteen minutes and if in the younger animals the reactions of the abomasum are still determined by the periodic ingestion of milk feeds the bulb is none the less full during the relevant active periods.

Perhaps the commonest form of activity is that described by Hagemeier. In this the first sign of impending motility is the development of a constriction across the wider part of the bulb - perhaps rather closer to the base than the apex of this part (fig. 74). This may develop slowly and be accompanied by a general slight contraction of the distal segment of the bulb or it may proceed rapidly to a more energetic phase. In either case there suddenly follows a rapid and total contraction of the portion of the bulb lying beyond the constriction and this usually effects a complete evacuation of this segment, its former contents passing rapidly through the succeeding stretch of bowel as an elongated and usually irregular streak. The distance this travels without halting is not well defined: it may succeed in reaching the jejunum where it splits up into smaller portions but more commonly it becomes stationary before leaving the duodenum and in this case its later fate will be considered when the duodenum proper falls for examination.

At other times the evacuation of the duodenal bulb is complete and this too may be accomplished in more than one way. Usually there is a rapid and total contraction with an almost simultaneous obliteration of the whole cavity: alternatively one may see the passage of a peristaltic wave from base to apex and then the appearance simulates what one imagines would be produced by running the finger along the bowel, squeezing out the chyme. Once again the distance traversed by the former contents of the bulb is not constant. Often indeed the bulbar contents are projected just clear of its apex or perhaps not even this far and sometimes they partially return into the duodenal bulb immediately following the forward movement or after a short delay. If this retrograde flow takes place it rarely succeeds in entirely refilling the bulb and the column generally splits into two separate fragments.

As though this variety was not enough there is a further aspect which requires notice. In addition to these effective contractions there are often to be observed others which develop, persist and then fade, apparently without achieving any object. These consist of localised or more extensive contractions which remind one of the segmental movements that are seen more distally but which unlike them rarely develop to a sufficient degree to interrupt, or even threaten to interrupt the continuity of the lumen.

At times the duodenal bulb establishes a rhythm of contraction apparently involving only its longitudinal muscle layer and this is manifested by a longitudinal expansion and stretching repeated some ten and fifteen times a minute and sometimes enduring for five to ten minutes at a time without interruption and without interference from other activities. This is commoner in the younger animals than in those over two months.

Reflux of the duodenal contents into the abomasum is a comparatively rare event and one which apparently is always associated with activity of the antral region of this organ. Indeed it is difficult to be certain that it involves any active participation of the duodenum itself and that it is not merely the result of the dropping of the intra-abomsal pressure below that prevailing in the bulb. It has previously been stated that the opening of the pylorus and the emission of the ingesta coincided with the intermediate phase of antral contraction and that the exit from the stomach normally closed before the antrum suffered the full systole. Imperfect co-ordination of these activities would permit the reverse flow without requiring any active movement of the part of the duodenum.

Turning now to the activities of the remaining stretch of the duodenum, it will be recalled that it is less constantly visible. Often enough it contains a few scattered pools or merely drops of the food and comparatively rarely is it portrayed in its length or when it is occupied by a continuous column of the ingesta. Little may be said about its movements when it contains only the scattered fractions. These are sometimes stationary for lengthy periods but when they move they travel fast and appear to thread in and out, following a complicated course round the portal flexure, and rapidly traversing the horizontal loop. One may assume that these appearances are due to the rapid movement of a localised peristaltic contraction but the ingesta themselves show little sign of whatever force propels them and leave behind no trace of their passage beyond an occasional drop or blob of barium.

When there is a more general filling of this organ it is easier to determine the nature of the movements: but these are then so complex, so variable and the form of the gut so mercurial that they almost defy description. Certainly the series reproduced in fig. 75, plate 12, will give a clearer impression than will the following account. It will be observed that the gut consists of segments of varying length and calibre some merging with their neighbours, others joining abruptly. Of these segments some are smooth walled, others indented by stationary or travelling contractions: some are of regular density and presumably of symmetrical section, others are irregular and these may be assumed to correspond with portions partially collapsed and distorted in section. So much is seen from a glance at the screen or on scrutiny of one plate: if the examination is extended to embrace a series of exposures it is seen that all is constantly changing and that the ingesta are shunted back and forth: as one part expands, then another contracts; as one lengthens, another shortens: sometimes a definite separation appears and the gap then closes once more: at times the bulb is emptied, a moment later it refills: and all the time the gut appears to writhe and twist, yet without effecting the displacement of the head of the column along the digestive tube. The kaleidoscopic effect may persist for some time and then suddenly and apparently without notice the column splits up, the distal parts sweep along the gut and into the jejunum and there break into yet smaller fragments while those that are left behind remain stationary for a time before one or other of these diverse activities again develops.

This description perhaps represents the extreme appearance and more often the activity is less remarkable. It is rarely possible however to classify the duodenal movements neatly under the headings of segmentation or peristalsis.

Discussion.

The mechanics of the duodenum have received relatively little attention even in man and the papers that are available, and the textbook references to the subject, indicate a remarkably diversity of opinion so that it is difficult to compare the different versions to much purpose.

It is, of course, necessary in the study of the problems involved to maintain the distinction between the duodenal bulb and the succeeding portion and in fact many have preferred to consider the former part with the stomach, with which it has an intimate functional association; the expression 'Nachmagen' is occasionally encountered while many refer to the remainder of the organ as the duodenum proper. In the goat, and also in the dog (Mecray 1941) where the bulb is poorly differentiated, this division is certainly too rigid for as has been seen the whole organ may be involved in a common pattern of behaviour.

The association of antral, pyloric and bulbar activity has already been remarked when discussing the activities of the abomasum but it must be stressed that in the goat independent activity of the bulb is by no means rare and may have no correlation that can be detected with the movements of the stomach. The description of Schinz, Baensch, Friedl and Uehlinger (1954) may be taken as representing the consensus of recent opinion of radiologists concerning bulbar mechanics: according to this authority the activity of the bulb may be systolic or peristaltic and in either case is generally total in nature. In the goat the fractional discharge of the contents after the manner described by Hagemeier is at least as common as complete emptying and in general it appears that the reactions of this part of the gut are more variable in the ruminant.

It has not been easy to determine whether there is any distinction to be observed at different ages. In the human infant (Henderson, 1942; Bouslog, Cunningham, Hanner, Walton & Waltz, 1935) and also in childhood (e.g. Caffey, 1956) there are certain morphological and functional peculiarities. The shape of the human organ appears to be generally spherical or cylindrical in early life in place of the more usual conical form of the adult but a similar difference has not been apparent in the goats: on the other hand it is stated that the bulb is more rarely observed in children since it reacts very quickly and promptly ejects the food passing from the stomach: there is possibly a similar trend in the kids but certainly it can be put no more strongly than that. The point is of course obscured by the intermittent discharge in the young and the continuous process in the older goats. Accounts of the gut mechanics of other species usually maintain a discrete reticence on these points.

The activities of the remainder of the organ display an even greater variety and according to most authorities resemble those of the succeeding parts of the small intestine, limited in the range of the more vigorous movements by the restrictions of the meso-duodenum. McLaren, Ardran & Sutcliffe (1950) record progressive and non-progressive segmentation, localised, single or multiple, contractions which may be fixed in location or mobile, and incisural indentations. They also stress the dramatic and complex changes in appearance produced by the activity of the mucosa and since this last feature is stressed in most accounts of the human duodenum it may be emphasised again that it has no parallel in the goat. Golden (1950) also states that mucosal changes are not apparent in animals but he refrains from indicating to which species he refers: personal observations suggest this absence in the dog, piglet and foal. The other activities mentioned are all recognised in the goat and in addition frank and unequiv-

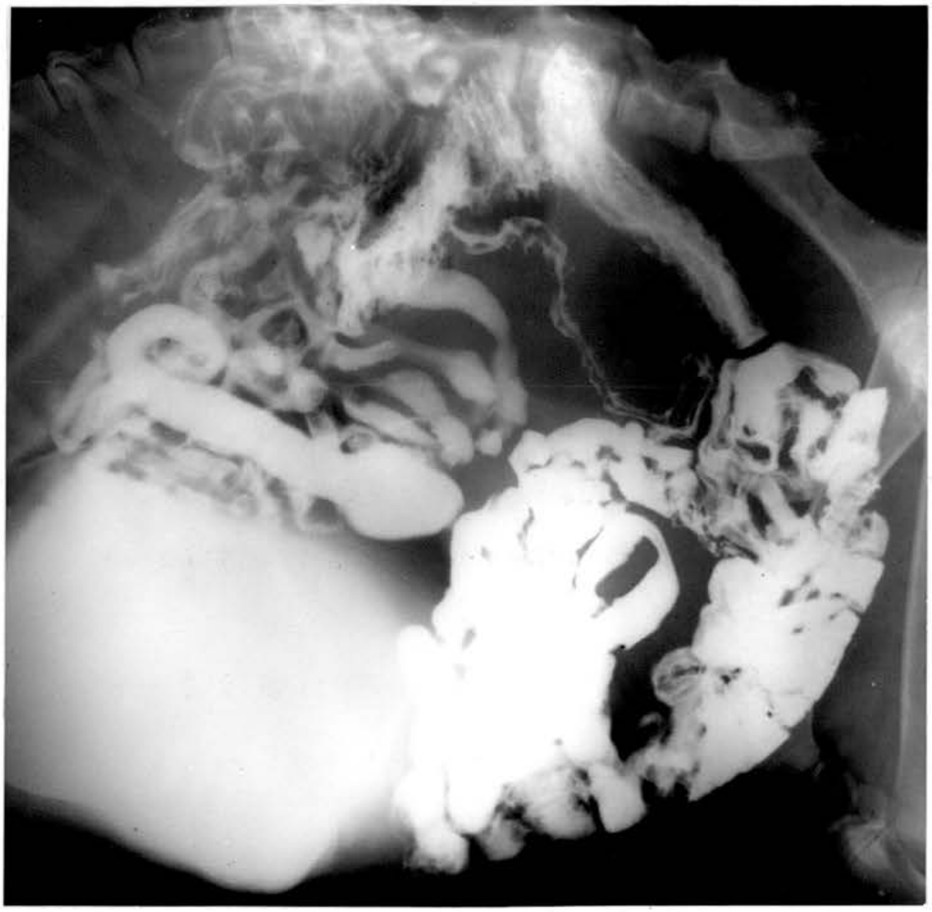


Fig.74 This film presents several unusual features: first, the shape of the duodenal bulb - ovoid and abruptly joining a long cylindrical portion of wide calibre: a very diffuse filling of the proximal jejunum with prominent mucosal markings: other markings of the more distal part of the small intestine including the long and almost empty terminal part of the ileum which for much of its length shows two parallel streaks - mucosal rugae or marginal filling with intermediate collapse? The small intestine had discharged into the large bowel about five minutes before this exposure was made. The large intestine resembles that in the preceding film.

Other views of the small intestine are shown in figures ocal peristalsis has been seen in this animal: most but not all authorities deny its occurrence in the human duodenum and Mecray concurs in the majority view after a study of the duodenum of the dog.

The paper of Mecray is perhaps especially important since he injected Thorotrast below the covering peritoneum in order that he could correlate internal and external alterations in outline. The commonest changes he observed in the canine duodenum were of a pendular nature and consisted of shortenings and lengthenings of the gut accompanied by rotation about the axis: the effect was very striking and produced characteristic writhings and twistings. He also observed that the lumen was rarely fully distended and that when ingesta passed only in small quantities they usually followed one or other margin of the shadow: the keyhole simile was suggested by this author. When the food passed in increased quantity the gut dilated to receive it but purely in a passive manner. Stationary masses of ingesta were retained by slight constrictions at either end but, this apart, there was no evidence of anything approaching segmental movement.

From this it may be concluded that the duodenal movements of the goat while showing no features not described in other animals are more diverse than those recorded for most species.

The Jejunoileum.

Radiological Anatomy.

General Considerations.

The remainder of the small intestine lies in the right half of the abdomen supported by the periphery of the common mesentery in which it forms numerous coils that partially circumscribe the large bowel (fig. 24). In general the course of the jejunoileum follows an extensive arc which commences in a craniodorsal position and sweeps first ventrally then in succession caudally, dorsally and finally once more cranially to enter the caecum in the upper half of the abdomen: frequently a portion lies within the pelvic cavity. Individually the coils show little constancy of position and it is quite impossible to trace the exact course of the small intestine as the relative mobility of the convolutions permits the displacement of some of the more proximal portions behind succeeding loops. The terminal portion of the ileum is relatively straight and runs without other than minor deflections towards the junction of caecum and colon (fig. 74). In radiographs the coils vary considerably in calibre, outline, the appearance of their content and in the duration and timing of their fullness: normally not all are shown at once. As a rule the food passes relatively rapidly through the first part which is

Fig.76 Subject aged four weeks, 2½ hours after feeding. Observe the great irregularity of the poorly filled proximal coils and the dense ribbon of the middle and distal sections which prevent a similar appearance to those in the preceding illustrations.

The dorsal irregular shadow represents the caecum and first part of the proximal loop of the colon: it is poorly filled and certain striations indicate a rugose formation of the mucosa. It is possible that the sacculated part of the small intestine lying below this represents the terminal ileum.

thus irregularly displayed but slows in its passage through the more distal portions which tend therefore to produce larger, more even and more persistent shadows.

In the first part of the jejunum the food rarely forms lengthy columns but commonly appears as irregular blobs of which the central region is relatively wide and dense and which taper to either extremity: commonly the tapering ends are of considerable length (figs. 53, 70 and 76). Elsewhere the outline may be more continuous but usually in these circumstances it is very narrow and the shadow of low density giving the appearance formerly described for the duodenum where it suggested an incomplete filling of a large collapsed tube (fig. 75, plate 12). Occasional patches of more turgid appearance are encountered and these may be marked by indentations, asymmetrical or encircling as the case may be.

In the middle section of the small intestine the coils tend to be more continuously filled and then they appear as a tangled and dense mass of overlapping and intermingling segments which are incompletely filled: this region will usually show evidence of the motor activities which are shortly to be described (figs. 71, 74 and 76). Finally, in the caudal section the coils may appear as continuous, relatively wide ribbons, which, apart from the constrictions that indicate activity, are of even outline: the density of the shadow is normally considerably greater in this region than in the parts that went before (figs. 70, 76 & 88D, plate 14). It will of course be appreciated that the division of the intestine into these three sections although convenient is quite arbitrary and that they do in fact merge one with another by imperceptible degrees. They correspond however in a very loose and general way with separate zones of the abdominal cavity. Variations on the pattern are exceptionally common and some of the diversities may be seen on comparison of figures 70, 71, 74 and 76.

The form taken by the lining mucosa is rarely greatly in evidence. If traces of the contrast agent remain in collapsed sections of the small bowel longitudinal striations may appear: in the more proximal sections these are faint and rather irregular but as the distal parts are approached they seem to increase in clarity and in regularity and may on occasion form a very striking feature (figs. 71 and 76): frequently two roughly parallel lines are visible and at times one is left in some doubt as to their exact nature (fig. 74): an alternative interpretation, namely that they represent thin streaks of barium lying along the margins of the bowel which is centrally collapsed, comes to mind. It will be noted that though on occasion the food entering the small intestine still retains signs of the breaking up of the milk coagulum the particles soon lose their individual form and the shadow becomes homogeneous (figs. 88A-C, plate 14).

Postnatal development.

In the neonatus the space occupied by the festoons of small intestine is relatively great and they have an extensive contact with both flanks, but especially the left, and with the abdominal floor, especially in the posterior part of the abdomen and when the abomasum is contracted (figs. 14 and 48). When the abomasum fills these coils are naturally displaced caudally. With increasing age they are denied access first to the upper part of the left flank (fig. 17) and then, with the further increase in ruminal capacity, to all but ventral and caudal strips of this side of the body wall until finally they are entirely disposed on the right. They continue for a time to occupy a great part of this side of the abdomen but later they are forced backwards by the developing omasum and upwards by the rumen (fig. 24).

Jejunoileal Motility.

Previous literature.

The authorities who have reported on this subject are those previously cited for the duodenum.

Czepa & Stigler in their first paper (1926) merely noted the occurrence of peristalsis. Later (1929) they stated that the small intestine always appears as a collection of irregular fragments of various size and never takes the form of a continuous band or column. They believed that pendular, segmental and peristaltic movements all occur but were unable to observe them on the fluorescent screen. Hagemeier (1937) provided a rather fuller account. He described the contents of the first part as spherical or spindle formations which sometimes appear at rest but which often move rapidly fusing and again dividing in quick succession and this he interpreted as evidence of segmentation and pendular movement. The activities become progressively less rapid as the caecum is approached and the more distal convolutions form a dense shadow. The contents appeared also to traverse the small bowel rather more slowly in animals of two or three months than in those twice this age.

Dukes & Sampson (1937) based their observations on the laparotomised animal. They described rhythmic segmentation as the commonest activity and also observed pendular and peristaltic movements with peristaltic rushes mainly responsible for the progress of the ingesta. But as they did not hesitate to stimulate activity by sprinkling the gut with a solution of barium chloride these observations must be accepted with reserve.

Observations.

The arrangement of the coils makes the study of their activities extremely difficult since it is rarely possible to follow a mass through any length of the bowel before the intricate path and the crossing of other shadows cause one to lose track of one's quarry. A few observations of a relatively general nature may however be permitted. Attention has already been directed to the fragmentation within the first part of the jejunum of the relatively large quantities of ingesta which sometimes reach this location from the duodenum (fig. 70). The masses formed in this way are of very variable size ranging in length from about half to five inches with a tendency for the shorter streaks to predominate. Usually they have a rather fusiform appearance and their tails may establish a tenuous connexion with their neighbours but others are quite isolated. If one of these is identified when stationary it will often be seen suddenly to commence a rapid passage which takes it on a very convoluted and irregular course, threading in and out, back and forwards across the paths of other shadows. It may halt without warning and then occupy a piece of bowel previously empty or it may join the hind extremity of a preceding mass. When this new formation moves in its turn it may proceed as a single unit or it may detach one or more fragments in rapid or more deliberate succession. So far this description has suggested that but a single quantity is in motion at a time but while this may well be the case, at other times many fragments will be transported simultaneously and then it is almost impossible to determine the identity of each for all appear in motion at once describing a most complex pattern upon the fluorescent screen. It is quite impossible to form a useful estimate of the distance travelled at each burst since a progress of a few inches through the abdomen may correspond to a length of gut of many times this length. Usually the ingesta leave behind no trace of their passage but a thin line may continuously indicate the length of the bowel and it appears that this is more often formed by deposit from previous fractions than as an extension of the advancing column (fig. 76).

In the middle section of the small intestine, corresponding to the ventral part of the flank, the shadows gradually become more continuous as the first material to gain this level is augmented by the arrival in succession of further quantities and this part of the gut may be marked by a series of constrictions spaced at rather irregular intervals (fig. 71). These identations may be quite sharply defined or they may be more extensive and gradually widen at either end where they join portions of greater calibre: but in either case they are formed and effaced and again recur with some rapidity (fig. 77, plate 13).

The terminal third or so normally shows an almost complete filling and since the coils are so closely mingled it is difficult to determine the nature of the movements. If a coil can be isolated from its fellows it normally demonstrates the segmental contractions and in this region these appear to be rather more regular than in the earlier section of the gut (fig. 70). The passage of ingesta into the caecum has rarely been observed but usually it appears that successive small portions of the ileum, corresponding to the length marked out by the segmentations are emptied into the large bowel. Sometimes however a more massive movement occurs and the last foot or so of this gut empties in a rush. This certainly occurred shortly before the film reproduced as figure 74 was obtained.

Retrograde filling of the small intestine from the caecum or colon has not been noted but in view of the difficulties attending precise observation no importance can be attached to this purely negative finding.

Discussion.

It is not proposed to discuss these findings at length. The normal movements of the small intestine recorded in the classic description of Hukuhara (1931) are segmentation, pendular movement and peristalsis of varying degrees of intensity. There is no doubt that the first and last of these movements occur in the goat and that peristalsis predominates in the initial section of this animal's small intestine and later gives way to segmentation as the principal activity in the intermediate and final parts. Pendular movements have not been recorded but the layout of the bowel and the difficulty of securing complete immobility of the subjects have combined to make it impossible to express a firm conviction that they are in truth absent.

Variations in the form and relative frequency of these movements are known to occur in other animals: Hukuhara himself records more frequent peristalsis in herbivores (rabbit and guineapig) than in carnivores (dog and cat) and also greater pendular activity in these species. He notes many species variations in the exact form of the movements. Krzywanek's (1927a,b,c) observations are in general confirmatory of these conclusions. Neiemeier (1939) describes pendular and peristaltic activity in the pig: Hill's (1952) findings for the horse are of a similar nature. The description of the human small bowel are more contradictory but all the forms enumerated have been recorded by one or other observers in man (see authors quoted for duodenum). In the face of these observations it is probably unwise to attempt any correlation of the diet and general structure of the alimentary canal with the types of activity the small intestine displays: certainly so far as the dietetic factor is concerned it may be said that no difference in the activities of kids of different ages has been recorded.

So far as one can tell the description that Barclay (1939) provides of the emptying of the ileum into the human caecum, with the occurrence of rapid rushes superimposed upon the normal churning movements, accords with the very limited observations made in the goat.

The general observation that the activities are energetically conducted in the proximal section of the gut and fall off in force as this is followed distally, agrees with the 'Gradient Theory' of Alvarez (1948) which receives further support in the following account of the large intestine.

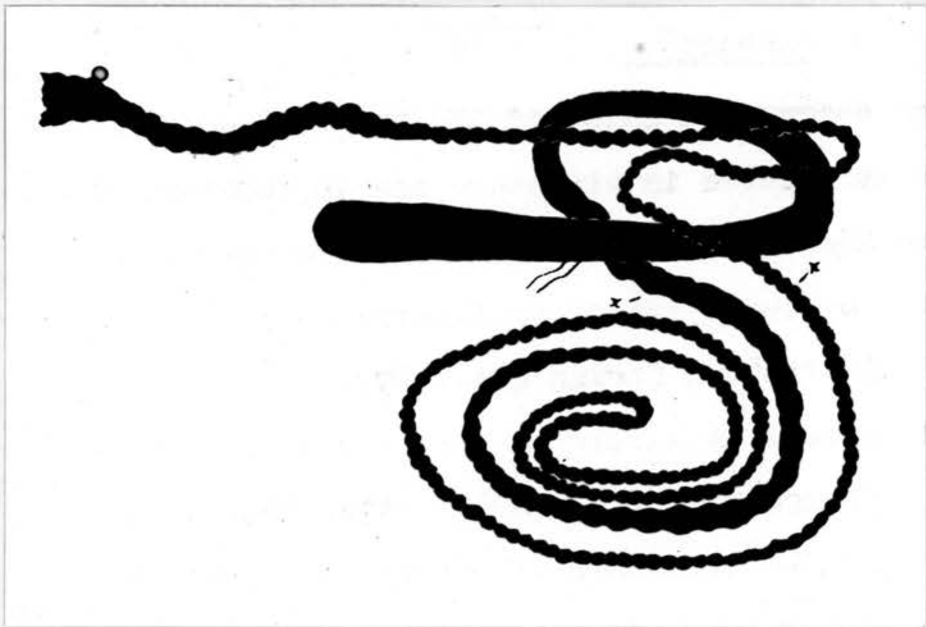


Fig. 79 Schematic representation of the large intestine as seen from the right. The ansa spiralis extends between the points marked. Note the change in calibre and contour of the various parts of the colon.

The Large Intestine.

Radiological Anatomy

General considerations.

The caecum and colon of the ruminant are so closely associated in structure and in function that they are best considered together. The general arrangement of these organs is schematically indicated in the illustration facing (fig. 79).

The caecum is simple in form and appears as a caudal prolongation of the colon (fig. 84). The greater part is contained within the mesentery which these organs share with the jejunoileum but the expanded free extremity is free and thus permitted a greater mobility. In the adult animal the caecum lies some way below the abdominal roof and to the right of the rumen: its general disposition is horizontal but its apex may be elevated or depressed, its position apparently being influenced by the nature of its content since it is common to find it raised when containing gas and pendant when filled with the heavier ingesta.

Usually its contour is smooth and its junction with the colon unmarked by any feature other than the entrance of the ileum, a point not often identifiable with certainty in radiographs. At times however there is a slight constriction at this level and similar contractions may indent the contours elsewhere.

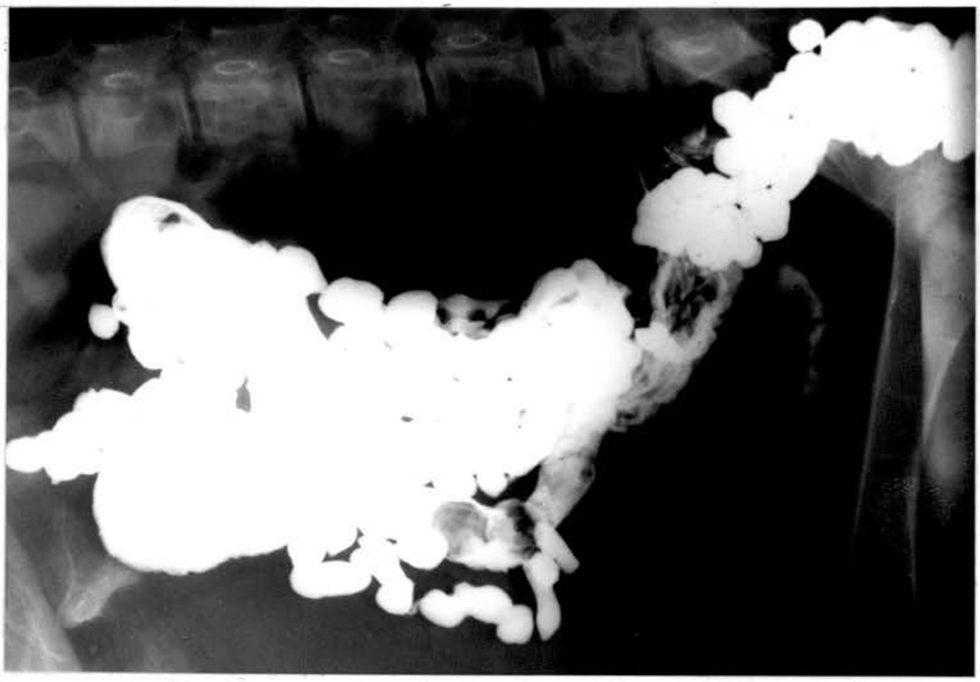


Fig.80 This radiograph is included to demonstrate the longitudinal striations that are sometimes apparent in the caecum and colon. The apex of the caecum contains very little barium and is distinguishable with difficulty. The parts of the colon are not readily identifiable. Observe the formation of the haustra and the calibre of the rectum.

The caecal shadow is usually of even density but occasionally it may present an elaborate marking (fig. 80). This is most apparent when the organ is contracted and contains only a small quantity of contrast substance which adheres to the mucosa or when it is partially filled with material of little radiodensity. On these occasions the most prominent markings run longitudinally and commonly continue into the first part of the colon: they are joined by an irregular pattern of oblique and transverse lines and presumably these indicate folding of the lining mucosa.

The colon is less easily studied since the coils usually lie one upon another and their continuity is lost (figs. 81 and 82). At times however almost the entire course may be traced. The following are the features that may be observed when conditions are most favourable. The part which continues from the caecum may be termed the ansa proximalis and this runs forward before looping round, between its origin and the stomach, to continue ventrally to enter the central spiral convolutions (fig. 84). The ansa proximalis tapers gradually towards its termination and is smooth walled except in its final section which shows the serial constrictions that become so much more obvious later (fig. 82). Like the caecum, and usually at the same time, the first part of the

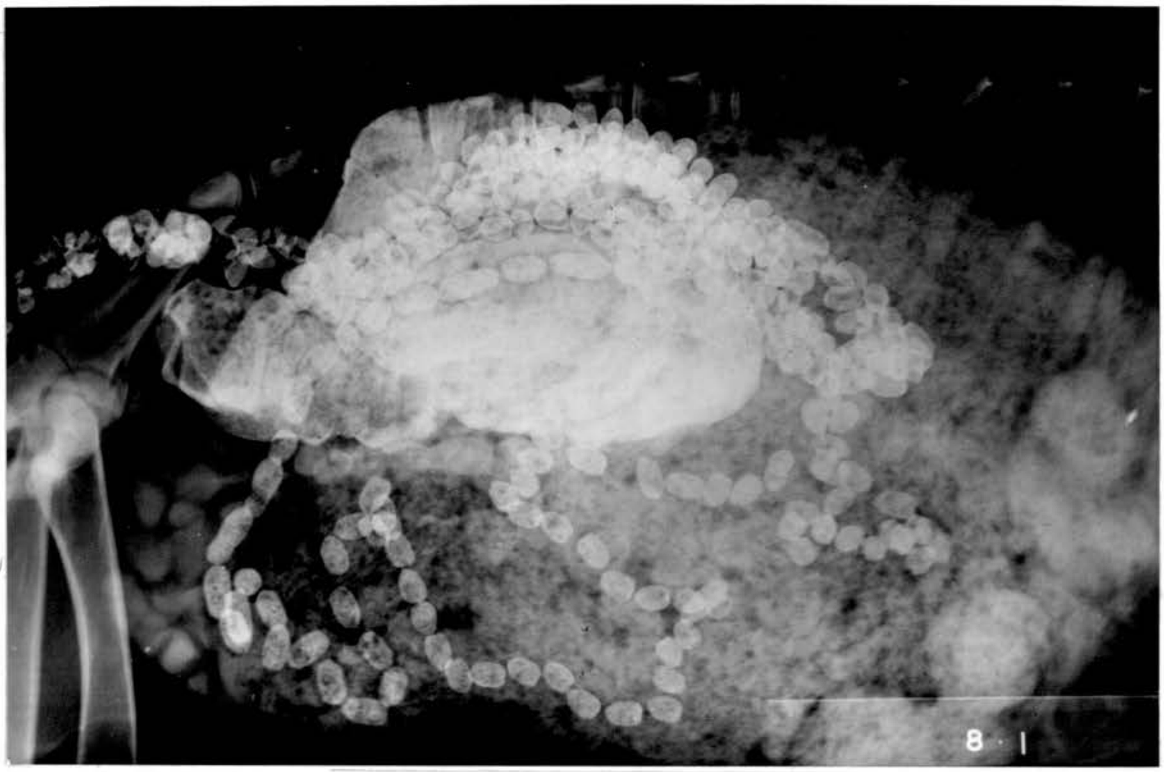


Fig. 81 The principal features to observe in this radiograph of the large intestine are the varying size of the haustra of the emergent coil of the ansa spiralis, some of which are of 'double' appearance, and the marginal corrugations of the caecum.

Small intestine will be observed behind the rumen.

ansa proximalis may present a mucosal pattern (fig. 74).

The ansa spiralis which continues this loop forms the most distinctive part of the gut. It first coils centripetally, then centrifugally in the manner shown in the diagram: commonly there are three turns in each direction. Occasionally the coils are arranged in an almost vertical series one above the other but more often the pattern is obscured by superimposition. The emergent loop is almost always clearly shown for it is long and loose and is liable to range widely within the abdomen (figs. 31, 81 and 82). On closer inspection it will be found that certain serial changes affect the spiral colon as it is traced distally (fig. 82). The first part is relatively wide but it tapers gradually as it approaches the apex of the coil and thereafter it maintains a uniform and rather narrow calibre. It is marked off into regions of variable size by constrictions that gradually become more prominent and more closely spaced until finally a chain of oval or rounded shadows is produced, reminiscent of the pellets that later appear in the faeces, although in fact the division of the digesta in these pockets is not yet permanent. In older animals the chain is continuous but considerable individual variations affect the size and shape of each link (figs. 81 and 82). Sporri & Asher (1940) have drawn attention to the narrow connexions that

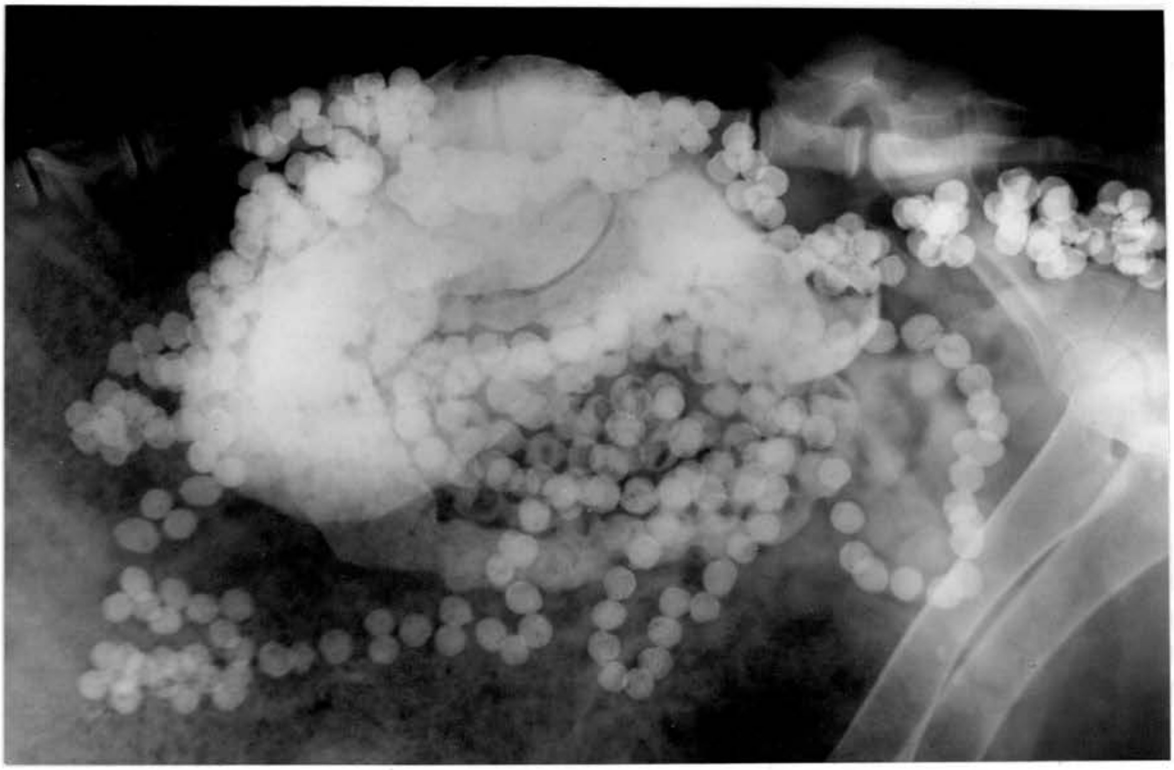


Fig. 82 The large intestine. In this film note particularly the gradual formation of the haustral pockets as the first centripetal coil of the colon is traced ventrally then caudally. The last centrifugal coil is, as usual, exceptionally long and convoluted.

In this, as in other films in which the colon overlies the spine, it is evident that the animal was recumbent.

join apparently separate shadows and their interpretation of this feature is considered later (figs. 31, 81 and 85).

The part emerging from the spiral forms the ansa distalis. This first passes caudally before running forwards to the region of the right kidney: thence the colon proceeds towards the pelvis, perhaps forming a flexure, the sygmoid flexure, about the entrance to this cavity in which it joins the rectum. It will be observed that in this last, descending, part and in the rectum the faecal pellets or scybala are arranged in several tiers (figs. 81-4).

The arrangement of the coils varies considerably in different individuals and in the one animal at different times. Smith (1955) made extensive observation of their disposition and concluded that in the adult the loops are too tightly adherent to the mesentery to enjoy much freedom of movement. Radiographic study suggests that their liberty is greater than postmortem inspection indicates and the general layout of the colon is rarely stable for long (see, for example, plate 2, figures D & E, in Benzie & Phillipson (1957). The general position of the colon is in relationship to the rumen and to the upper and central parts of the right flank, the anterior extremity of the convolution lying below

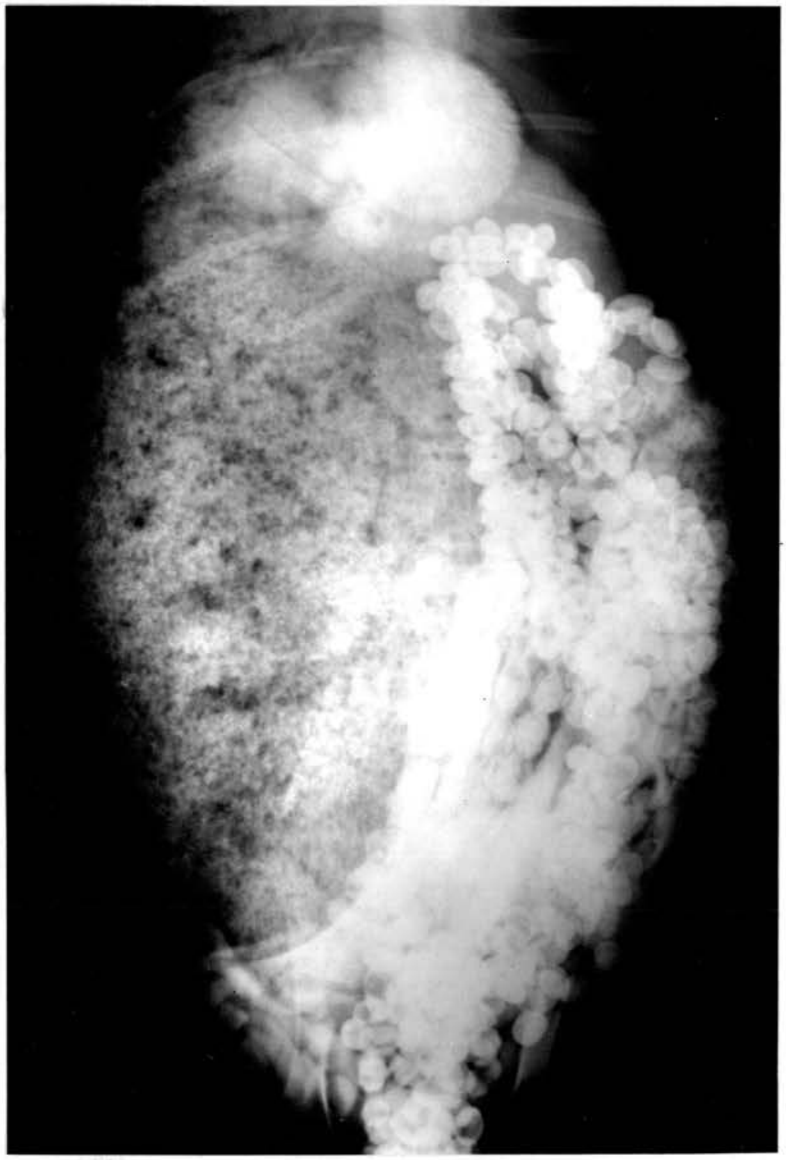


Fig.83 Dorsal view showing the relationship of the large intestine to the rumen at 8 weeks.

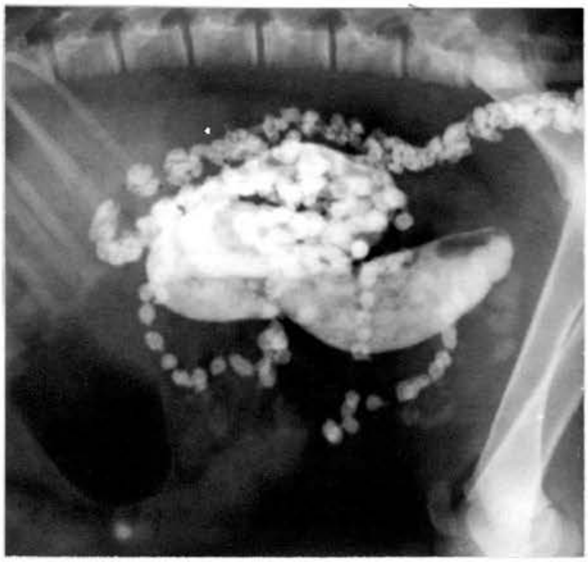
the last few ribs (fig. 83). The final centrifugal coil approaches and may even enter the pelvic inlet.

The relationship between large and small intestine has already been noted.

Postnatal development.

In the younger animals the large bowel occupies a proportionately larger part of the abdominal cavity than is the case in the adult and this reflects the undeveloped state of the stomach and the consequently shallow abdomen. During the first six weeks of life much of it lies to the rear of the rumen and the caecum in particular may achieve contact with the left flank in the earlier part of this period (figs. 17 and 19). At this time the caecum is exceptionally variable in its disposition and a vertical arrangement is common and brings the blind extremity close to the abdominal floor (fig. 85). Exceptionally the caecum is found facing forwards, a displacement that presumably requires the rotation of the entire mass of large intestine.

The migration of the large intestine to its adult position is brought about by an extension of the rumen and, coincident with this, a proportionate decrease in the size of the abomasum: correlated with these alterations the gut gradually rises in the abdominal cavity as the latter extends ventrally (fig. 56).



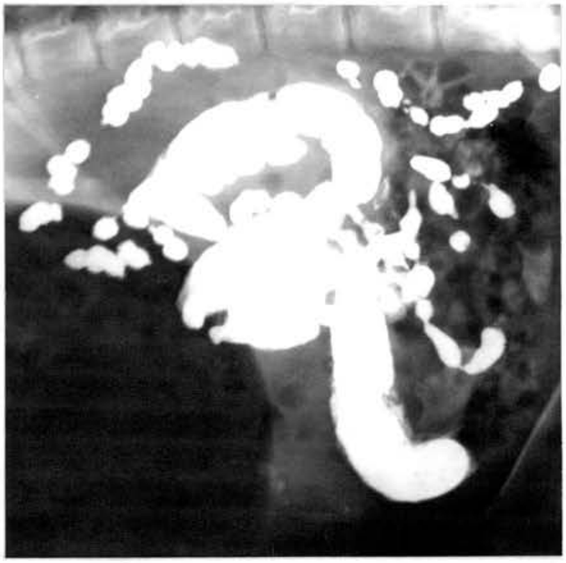


Fig.84 (left). Large intestine of a kid aged four weeks, 36 hours after feeding. The caecum lies horizontally with its apex, which contains a little gas, slightly elevated. The ansa proximalis is easily distinguished but it is not easy to define the coils of the spiral colon. It will be observed that the haustra are joined to one another by the small connexions mentioned in the text.

Fig.85 (right). Large intestines of a kid two weeks old, 24 hours after feeding and shortly after defaecation. The pendant caecum is easily distinguished but once again the colon cannot be traced through its convolutions. The colic contents are not continuous and this is a frequent observation at this age and while the breaks in the descending colon may have been occasioned by the mass movement that produces evacuation, those in the spiral are of prior formation. The haustra of the spiral colon are very irregular in extent and in many cases are again joined.

As a general but not invariable rule the mucosal patterns are rarely well displayed in the younger animals. The intermittent emptying of the abomasum of the milk fed animals results in a spacing of the ingesta through the later parts of the tract and a frequently incomplete filling of the colic coils (figs. 84 and 85). Small breaks in continuity, perhaps too slight to be accounted for in this way, are even more common in these subjects.

Motility.

Previous literature.

The movements of the large bowel of the ruminants have been mainly studied by means of X-rays and Czepa & Stigler (1926, 1929), Hagemeier (1937) and Sporri & Asher (1940) have contributed in this way: all used goats in their investigations. Dukes & Sampson (1937) made direct observations in laparotomized sheep.

The account of Czepa & Stigler is relatively short. They described the general appearance of the parts and noted that the contents became progressively thicker along the length of the colon. The caecum and first part of the colon show continuous peristaltic and anti-peristaltic waves while the succeeding section was characterised by tonic constrictions. The movements of the spiral part were so slow in execution that they could not be detected.

Hagemeier enlarged this description and noted the rapid filling of both the caecum and the proximal coil and the energetic shunting of ingesta to and fro between these parts. He also described segmental and weak peristaltic contraction of this first section of large bowel. He observed that the moulding of the faeces was produced by tonic contractions of the spiral coil.

The technique of Sporri & Asher, who produced the most important description, differed in one important respect from that of their predecessors. They produced caecal fistulae which permitted them to deposit the contrast agent at selected points and this allowed the study of particular segments unobscured by overlying shadows. Naturally this interferes with mobility of the caecum and initial part of the colon and they attribute to this their failure to recognise certain of the movements previously described. They describe three functional regions: caecum + most of the ansa proximalis: terminal ansa proximalis + ansa spiralis: ansa distalis + descending colon + rectum. The first part secures good mixing of the contents by means of to and fro shunting and segmental contractions and the initial thickening of the contents is achieved here. The second region shows peristaltic (but not antiperistaltic) contractions and rhythmic polymorphic segmentation with pronounced tonic constrictions (isomorphic segmentation) as the most characteristic feature: dehydration continues in this section. The third part demonstrates very slow migration of the tonic constrictions ('Haustrenfliessen'): the greater part of this region serves as a receptacle for the faeces awaiting excretion. They twice observed regurgitation through the ileocaecocolic opening. According to their experiments the time required for passage through the large bowel is 4-8 hours.

Dukes & Sampson's observations were largely confirmatory of the radiological evidence. They regarded the caecum as the main propulsive element and believed that it not only propelled the digesta through the ansa proximalis but provided the vis a tergo which assisted their passage through the spiral coil.

Observations.

The large bowel has not been extensively studied since the movements are very well described by others while the superimposition of the coils impedes accurate observation in the intact animal. Moreover the activities are either too slow or too spasmodic to be recorded in serial form.

A number of points may however be made. The passage of the ingesta into the large intestine is intermittent (vide supra). At times opaque material collects in the terminal ileum for upwards of an hour before receiving admission and the first quantity is sometimes joined by little or no subsequent fractions for an equally long period: on the other hand the ileum may discharge into the large intestine many times in close succession. Usually the contents of the last stretch of the ileum pass through in a rapid succession of very small fractions and after each burst of activity there is a spell of inertia. It is difficult however to be specific concerning these events since the relationships are often obscured by overlapping coils.

The incoming material is deposited about the iliocaecocolic valve and immediately commences to be mixed with the previous contents by repeated segmental and weak peristaltic contractions. If these persist for any length of time the extent of the part outlined increases in both directions and eventually the caecum and first half at least of the proximal loop are displayed. More commonly however these mixing movements are interrupted by the passage of a powerful wave of contraction which carries the digesta in either direction, probably rather more commonly towards the caecum. If such a movement supervenes promptly after the introduction of the first contrast fluid then only one or other of the caecum and colon will be at first apparent. These major contractions are irregular in their occurrence but normally they are separated from each other by no more than six minutes: those that carry the food in retrograde direction are frankly antiperistaltic in nature but the others which commence at the caecum seem also to involve a total contraction of this organ and they succeed in pushing the digesta through the entire loop of the ansa proximalis and apparently into the origin of the spiral coil which relaxes to receive the head of the column. The return of the food to its former position is incomplete and some ground is always gained.

The purely mixing movements in this first section are not very conspicuous. One of the commonest forms resembles the segmental contractions that are so obvious a feature of the spiral part but this activity is much less developed in the proximal loop and in the caecum, and commonly the constrictions do not divide the lumen to any extent. The more pronounced develop rapidly and disappear with equal suddenness after a very short duration but others of a less intense nature may persist for some time and may even remain during the course of the peristaltic waves which also run up and down these parts. Usually the latter are not well developed and appear merely as ripples of the margin of the bowel.

Independent activity of the caecum is also to be observed. This activity is characteristic and consists of systolic contractions which effect a discharge of varying amounts of the contents of the organ into the first part of the proximal coil which dilates to accommodate them. This isolated movement is not by any means common and systole is more usually accompanied by the peristaltic wave which was previously mentioned as supplying the main transport force.

The anatomical and functional borders of the succeeding spiral colon do not exactly coincide since the ultimate few inches of the proximal loop are indistinguishable in their behaviour from the first part of the spiral colon. These parts are marked by the tonic contractions which produce the characteristic effect and these may appear to be stationary or else moving slowly in a distal direction. There are times however when this part displays great activity and in place of the tonic contractions true segmental constrictions rapidly appear and disappear. These are the movements which Sporri & Asher termed the polymorphic segmentations since the parts they separate are of unequal size: on the whole the more proximal contractions are more widely spaced. Sporri & Asher describe how these contractions may be entirely effeced and the spiral coil converted into a smooth walled tube. In the present study this has only been observed over the proximal section - roughly corresponding to the centripetal coils - and at these times quite pronounced but irregular peristaltic waves may course distally over the tube:

but as suddenly as this activity commenced it disappeared and the segmental contractions returned.

Movement of the distal coil has not been recognised.

There are one or two minor points which may be noted and which appear to be peculiar to, or at least more common in, the young kid.

In these animals the process of dehydration of the faeces appears to be less efficient and the contents of the greater part of the large bowel more fluid than in the adult and it is perhaps because of this that the movements appear to be less vigorous and the indentations less pronounced in early life. It has already been observed that in the young animal the colic shadow may demonstrate relatively large interruptions and while some of the gaps appear to be the effect of the spasmodic emptying of the abomasum others doubtless result from the fact that the first part of the large bowel may itself discharge into the spiral coil intermittently.

It is more common at this age to find the caecum making an early appearance considerably before appreciable quantities of contrast material are to be found in the colon: from which it may be concluded that the retrograde movement is commoner than that in the opposite direction and that the vigorous to and fro movement between caecum and colon is in abeyance. None of these distinctions however persists beyond the first six or at most eight weeks of postnatal life.

Discussion.

The foregoing observations may be regarded as confirmatory of those reported by previous workers: indeed Sporri & Asher provided much greater detail concerning the spiral colon than could be observed in the unoperated animal. There is little need therefore for a prolonged discussion of the findings.

In summary the caecum was shown to demonstrate systolic, peristaltic and antiperistaltic, segmental and tonic contractions: the colon peristaltic and antiperistaltic (the latter in the first part only) and segmental contractions of various forms of which the flowing of the successive haustra and constrictions in the distal part is the most characteristic of the ruminants. All of these activities have been recorded in other species although it is notable that the pendular movements seen in some forms seem to be absent in the goat. The function of these activities appears to be obvious: as elsewhere (Trautmann, 1943) the tonic and segmental contractions may be regarded as effecting mixing of the digesta and this is probably the major significance also of the weaker peristaltic waves. The churning of the material within the bowel brings successive fractions into contact with the mucosal surface and hastens the absorption of water which is so important a function of the large intestine. The alternation of the violent peristaltic and antiperistaltic waves in the first section will have the same consequence and even in the caecum there can be detected a certain thickening of the contained material. According to Sporri & Asher the solid content of the digesta rises in this region from roughly nine to twelve per cent. The nergetic movements of this part of the large intestine are also responsible at times for driving the contents of the caecum and proximal coil into and some way through the spiral colon. More distally in the gut the movements are more specifically directed towards transport but it is easy to forget that the contractions that subdivide the lumen and produce the striking radiographic appearance are not permanent and that the final division of the digesta into the faecal scybala is not effected until near the termination of the ansa spiralis.

A passing allusion has already been made to the suggestion of Sporri & Asher that the formation of the haustra is produced by the folding of the mucosa membrane under the influence of the muscularis mucosae and they referred to the teaching of Forssell (1923) on the importance of the mucosal relief in the study of the function of stomach and gut. They first drew attention to the relatively wide gaps that separate some of the pockets and to the narrow streaks

(Ductus centrales) which are sometimes evident to either end of these formations and appear either as pointed projections or as thin links joing adjacent cavities. The external view of the bowel shows a far less distinct delimitation of the segments and it can be presumed that mucosal folds or septa mucosa are erected to assist the division of the lumen.

The argument appears convincing and it is thus important to distinguish the haustra mucosa seen in the ruminant from the superficially similar formation apparent in the large intestine of the horse, the haustrum musculare which is produced in the main by the contraction of the muscularis propria.

Fig.86 The liver of a kid aged 6 weeks, two days after the intravenous injection of 20 cc 'Thorotrast'. The shadow of the right kidney may be seen lying in the renal fossa above the caudate process. The abomasum contains a large amount of gas and is visible on the floor of the abdomen. The very dark shadow ventral to the caudate process represents the duodenal bulb.

The Other Organs.

The remaining organs of the abdomen have received very little attention and only incidental observations are recorded. A few features may however be noted.

The liver, though relatively denser than most other viscera is not depicted clearly in plain radiographs. Some idea of its entent may however be inferred from the appearance of neighbouring parts (e.g. fig. 50). In order to demonstrate this organ more convincingly one animal, aged six weeks, was prepared by the intravenous injection of 'Thorotrast', a preparation of thorium dioxide which is largely concentrated in the liver and spleen. This resulted in a more exact appreciation (fig. 86) of both these organs but the effect was not persistent and by three months little evidence of the presence of Thorotrast remained, although whether it was removed or merely diluted in the growing liver could not be determined. The experiment was not repeated since the injection appeared to have a deleterious effect and the subsequent growth of the kid was impaired. In adult and subadult animals the posterior border of the liver may be recognised without artificial aid.

The liver of the kid is contained mainly within the right half of the abdomen and lies with one surface related to the diaphragm and the other in contact with the various chambers of the stomach, the pancreas and the duodenum. The upper extremity carries a caudate process and between this and the main mass of the organ is a recess for the right kidney (fig.86). The liver is precociously developed in the foetus and in the newborn animal its size remains disproportionate to its adult bulk: at this age it is much thickened laterally and it extends considerably across the mid-line ventrally and also caudally behind the right costal arch (fig. 48). In the next few weeks it diminishes rapidly in relative size as is confirmed by the migration of the abomasum and by the extension to the right of the rumen and reticulum and already by six weeks only a small amount lies in contact with the flank (fig. 56). Further change to the adult proportions is gradual and is not well shown in the radiographs.

The gall bladder has not been seen. Attempts to demonstrate it, and also the intra hepatic biliary channels, following the intravenous injection of Biligrafin, according to the technique successful in man and in the dog (Dyce, 1956), have met with complete failure.

Most of the other abdominal organs were only occasionally visualised. The position of the spleen is sometimes indicated by an indentation of the ruminal shadow and this organ was also displayed following the Thorotrast injection but its appearance

Fig.87 This radiograph shows the bladder and indicates quite clearly that the diodone solution is excreted by the kidneys although these organs cannot themselves be demonstrated by means of intravenous pyelography.

has been too rare to permit useful discussion. The dissections indicated that like the liver it is disproportionately large in the neonatus and that it then extends far further ventrally than in the adult (fig. 14): its later growth is very slow: the position of its upper part remains unchanged at all ages.

The kidneys are occasionally depicted. The right one is related to the liver (fig. 86) and is fixed in position but the left one which at first lies to the left of the midline is more mobile and as the rumen increases it is pushed across to the right and also somewhat caudally. The period of this migration appears to vary somewhat but it generally occurs between six weeks and three months. Attempts to demonstrate these organs by means of intravenous pyelography have met with almost total lack of success and an occasional vague shadow, presumably in the pelvis, has been the most that has been visualised. The bladder however has been well shown (fig. 87) and its appearance suggests that it has been the inability to compress the ureturs and thus retain the dye in the pelves that has produced the failure.

Organs which have remained completely invisible at all times are the pancreas, the genital tract and the omentum and other fat deposits. On a future occasion it might be useful to assist their demonstration by the production of a pneumoperitoneum.

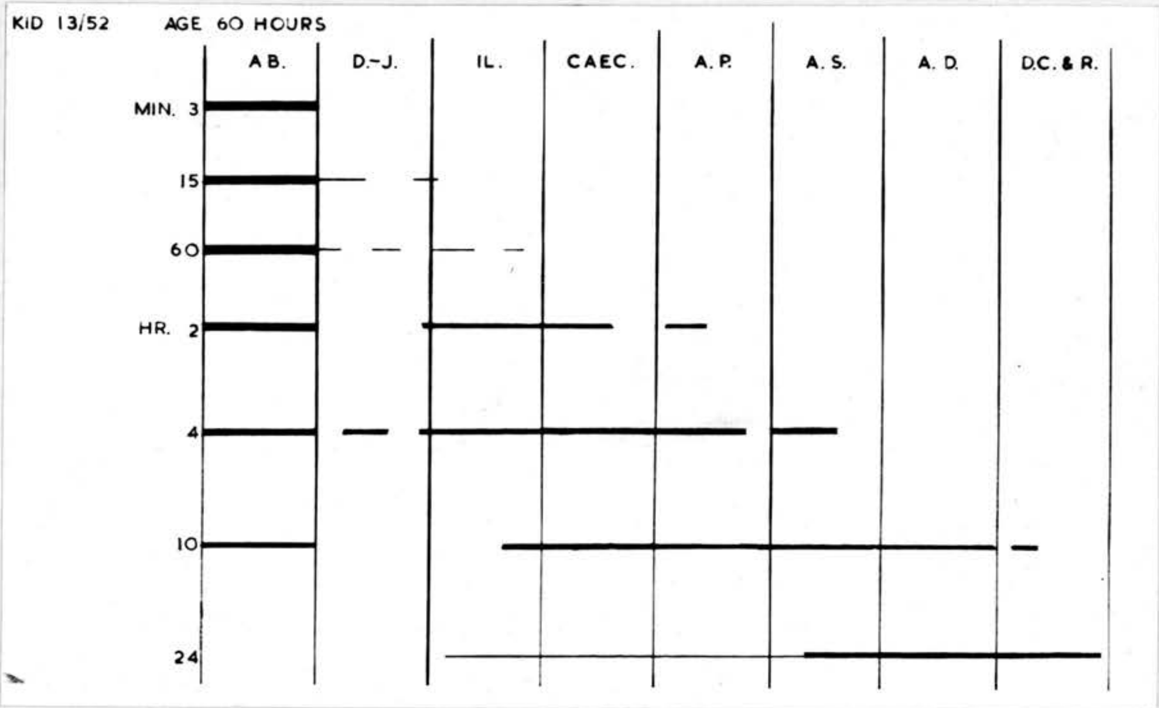
The Passage of Ingesta through the Alimentary Tract

The study of the rate of passage of the ingesta was not included in the original scheme of this investigation since to be of real value it necessitates systematic examination at frequent and regular intervals and must continue without interruption until the test meal has been eliminated. The first requirement is excessively restricting and interferes with the detailed study of special features as these arise, particularly when several animals are examined at a single session as was the custom, while the second presupposes the presence of sufficient assistance after normal working hours, an arrangement that was impossible save on rare occasions. Some information relevant to the topic has however naturally accumulated and a few observations may be permitted.

It might appear at first sight that the use of an opaque meal to trace the passage of food is peculiarly advantageous since it allows periodic determination of the position of the head and tail of the column in the intact animal. There are however certain drawbacks: the contrast agents employed for this purpose, salts of either barium or bismuth, are materially heavier than the ordinary ingesta - they owe their radio-opacity to their molecular weight - and have a tendency to settle from suspension with the result that they may not be transported at the normal rate. It is in fact unlikely that the movement of the vanguard of the meal is much altered, at least with the opaque products prepared for this purpose, but the effect cannot easily be measured and possibly varies from species to species and from organ to organ according to the force and regularity of the mixing and transport activities. This defect has certainly not prevented the use of radiological methods for this purpose in the human species and a similar application may be permitted in animals, with the proviso that comparison of the results with those obtained by other techniques requires caution. There is however one further drawback, important in work in the ruminant, which does not arise in animals with simple stomachs: this is the great dilution that takes place in the rumen, not only on first ingestion but increasingly with subsequent meals, which makes it exceedingly difficult and finally impossible to determine whether or not any of the experimental feed remains in this organ.

The observations recorded are extraordinarily variable and the analysis of the results if further complicated by the gaps in the records and by the varying circumstances of the examinations, particularly in respect of the usual feeding habits of the subjects, and the size and sequence of the contrast and normal feeds. It is probably best to give some

Chart 1.



The columns refer to the abomasum, duodenum + jejunum, ileum caecum, ansa proximalis, ansa spiralis, ansa distalis and descending colon and rectum.
The subjects of the first three charts received the meal from a feeding bottle.

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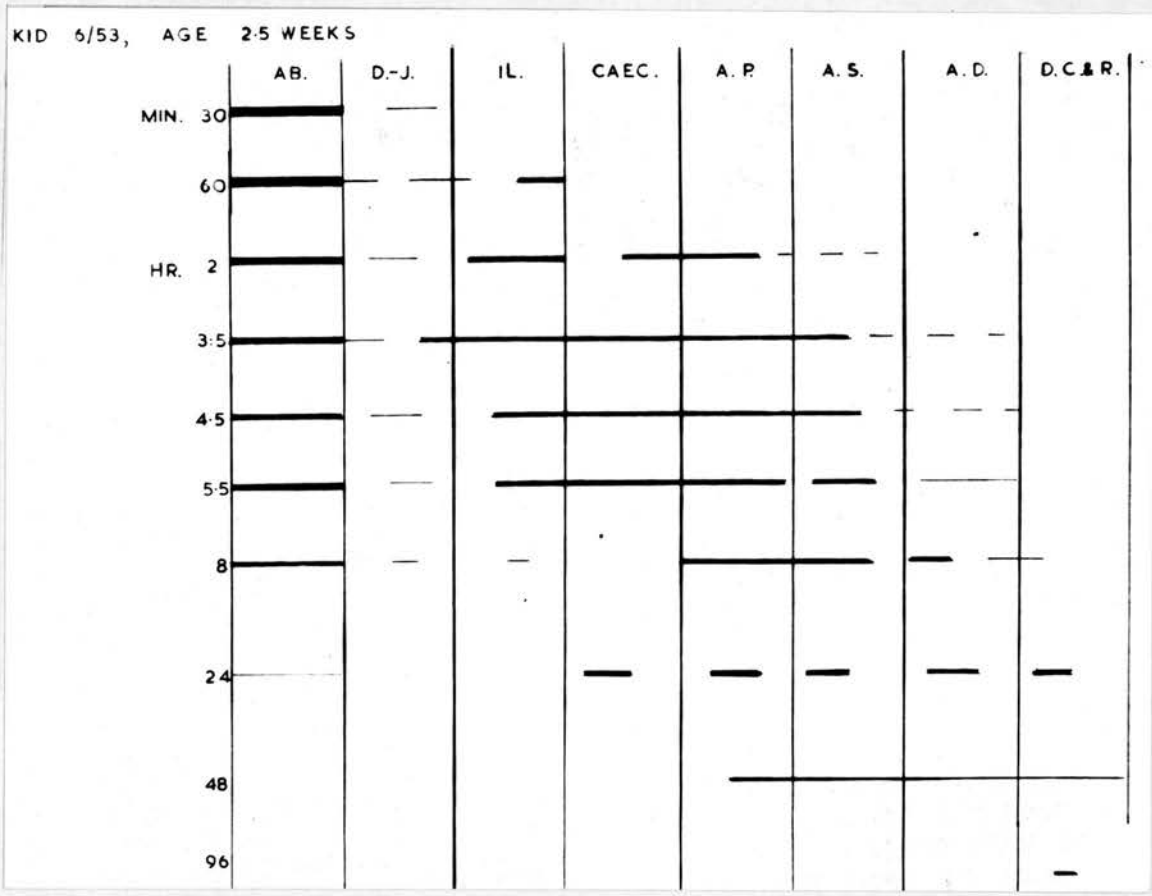
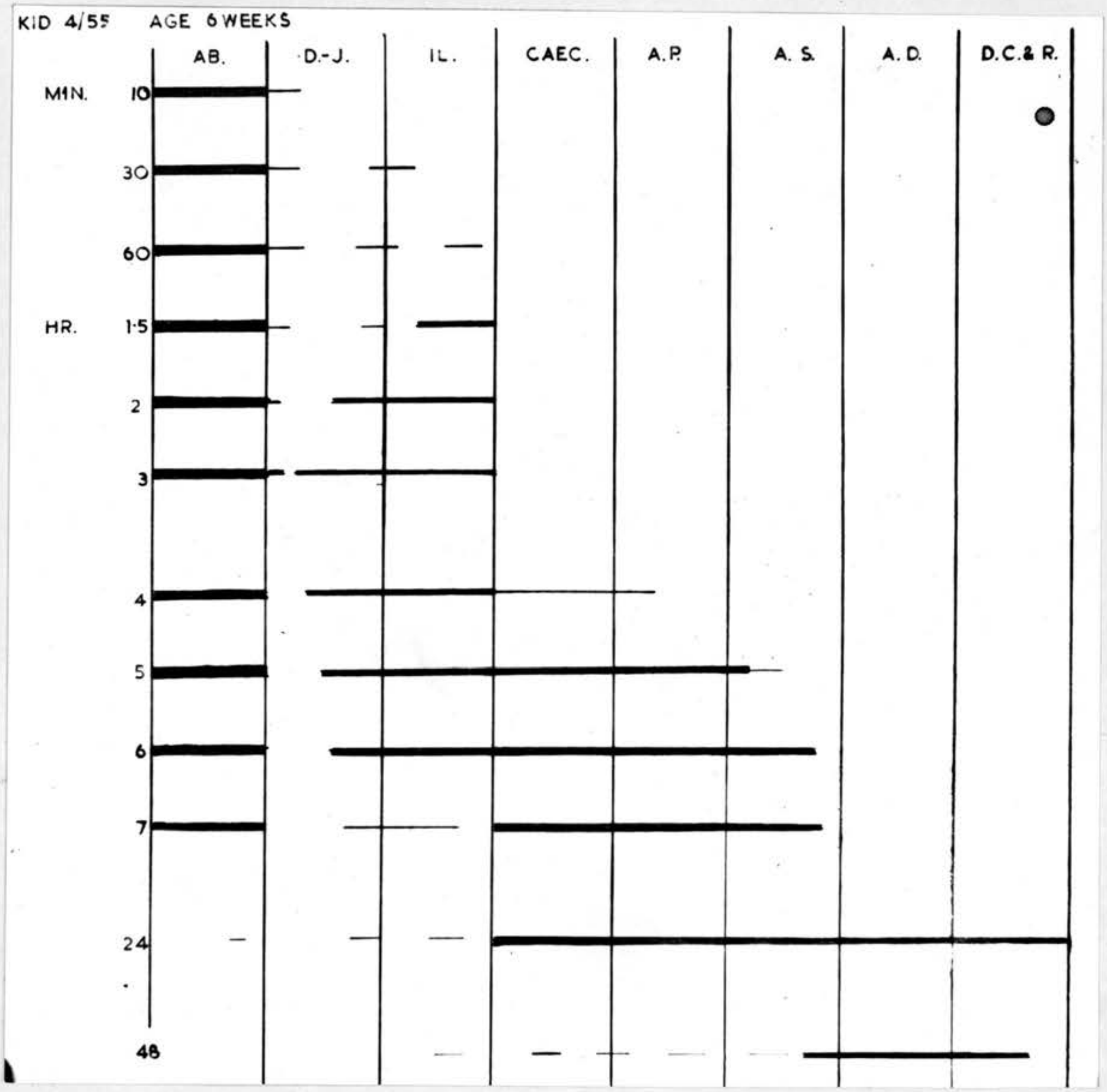
idea of the nature of the results before attempting to establish the existence of any general trends and this is most conveniently accomplished by the reproduction of a few charts indicating the pattern at selected ages: these will be found on this and the following pages.

Chart 2.



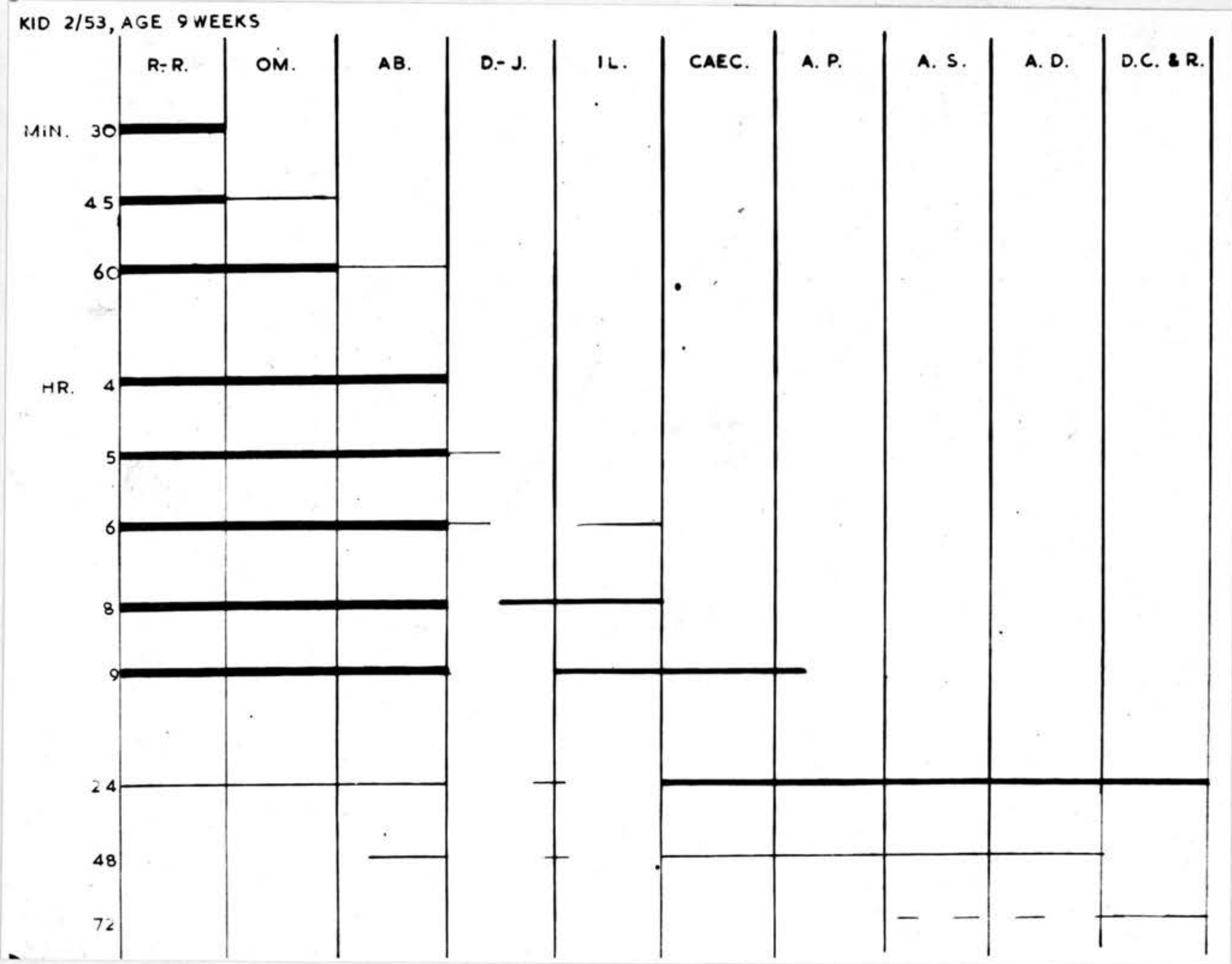
It is well known (e.g. Watson & Jarrett, 1944) that milk passes immediately into the abomasum in the sucking ruminant and some account of this process has already been given. The escape of the meal into the intestine is spread over a very considerable time although a small fraction passes into the duodenum within minutes of ingestion and the bulk is evacuated within a few hours: some will remain beyond this

Chart 3.



period and if mixed with subsequent feeds traces may persist for twenty-four hours or even longer. In consequence the head and tail of the meal may be separated by as much as a day before even the small

Chart 4.



The additional columns refer to the rumino-reticular sac and the omasum. In this case the opaque medium was delivered by stomach tube.

intestine is traversed. Transit through the small intestine is almost always rapid and requires little more than one hour in many cases and the appearance of the caecum is mainly determined, therefore, by the rate at which the abomasum empties. The time at which the caecum first appears is indicated in Table I.

TABLE I.

Kid	Age	Time of appearance of caecum (in hrs. after meal enters abomasum).
13/52	60 hours	1¼ - 2
2/52	4 days	2 - 2½
3/54	7 "	1 - 1½
2/52	11 "	2½ - 4
7/53	2 weeks	3 - 3½
6/53	2½ "	1¾ - 2¼
11/52	4 "	3 - 4
4/53	5½ "	2½ - 4
4/55	6 "	3 - 4
10/52	7 "	2½ - 4½
12/52	8 "	3½ - 4½
2/53	9 "	7 - 8
8/53	10 "	5 - 5½
2/53	14 "	4 - 6
1/53	16 "	3½ - 6
1/53	8 months	3 - 3½

The irregularities in this table - which is representative rather than exhaustive - show the difficulties of arriving at definite conclusions but a trend towards a slower rate of passage in the older animals may be discerned: in the neonatus little more than one hour is sometimes sufficient for the demonstration of the first part of the large intestine but this increases until in the older kids and adult goats upwards of three hours are required. The individual times are so variable and the feeding habits of the kids so diverse that it is not possible to determine either the cause of the change or the exact stage at which it occurs but since it roughly coincides with the adoption of a mixed diet it is difficult to resist the conclusion that the two events are related. One other point which emerges from these figures is the occasional exceptional delay in the appearance of the large bowel: since delay in passage through the small intestine has not been recognised this strongly suggests that at times there is a prolonged interruption in the emission of the abomasal contents in the older animals, although it is not necessary to question the general validity of the belief of Phillipson (1948) that the process is almost continuous.

Passage through the large bowel is slow. Usually the spiral coil is entered about one hour after the head of the column reaches the caecum and ansa proximalis but further progress is slow and by no means uniform. A very rapid passage will result in the appearance of the descending colon or rectum within four or five hours of this time but more commonly a minimum of six hours and more often eight, ten or even twelve will be required for the digesta to traverse this part of the tract. Much depends on the evacuation of the earlier feeds: if the distal part of the colon and rectum are distended and defaecation is delayed then the movement of the later digesta may be greatly slowed and eventually halted.

The effect of age on this process is not readily determinable: in the younger animals the movement appears to be very slow but it accelerates within the next few weeks as the intake of solid fodder increases. The individual timings are so variable and inconsistent that little purpose would be served by their enumeration. The bulk of the milk meal follows soon after the initial portion although a small part drags behind and affects the final elimination disproportionately: the large bowel is generally virtually clear within two days but minute traces may persist for another twenty-four hours or so. This statement implies that there is a retardation in the large intestine in addition to that seen in the abomasum and while this is in fact the case it is not possible to offer a convincing explanation of its cause: it may indicate an unexpectedly efficient mixing of the ingesta in this part of the tract with the contamination by the agent of the successive feeds as they reach this point or it may merely indicate a settling from suspension. It is unfortunately impossible to be more specific.

So far consideration has been given to the fate of the milk feed. The elimination of the contrast material which enters the rumen is a more protracted affair. An increased density of this organ is visible for at least two days and generally for longer: as the ruminal contents normally possess a considerable capacity it is difficult to be certain of the end point and it must be assumed that the last traces are not detectable by radiological methods. Since there is a further delay in the large intestine and as small traces are more evident in this part it follows that complete clearance of the abdominal shadow requires not less than five days.

Discussion.

Analysis of these results admits of few firm conclusions and the study of other reports is hardly more rewarding since no radiological investigation specifically designed to provide this information has yet been reported.

The rate of transport of the ingesta in the ruminant has been studied quite intensively by the method in which marker substances are fed and later recovered from the faeces. Most workers have been concerned with sheep and cattle but the goat has figured in the investigations of Columbus (1936), Biondo (1953) and Castle (1956a, b & c). In her first paper Castle gives references to work in the other ruminant species and these need not be considered further. Using this technique it is possible to determine the shortest and longest times the marker takes to traverse the tract and it is also possible to calculate the proportionate rate of excretion by suitable counting techniques. The time of the first appearance is fairly uniform - 11-16 hours is the range suggested by the workers named - and this corresponds to the passage from omasum to rectum, presuming an immediate escape from the first chamber of the stomach. The time of eventual disappearance is more variable; Castle (1956a) quotes 6-7 days, Biondo 11-17 days and Columbus 17-19 days. This great difference may in part be due to the different substances employed - Castle having used hay, the others straw - and it may be assumed that the extensive interval between the first and last appearances corresponds in the main to the sojourn in the rumen. A more exact division of the time the markers spend in the different sections of the alimentary tract is not possible unless fistulae are employed to enter the material at intermediate points, e.g. into the duodenum, (Castle, 1956c), or unless animals are slaughtered and examined at intervals after feeding. Castle found that material introduced into the duodenum of mature goats appeared in the faeces in 9-12 hours and attained a maximum concentration one or two hours later but naturally she was unable to divide the time of passage into fractions corresponding to the several sections of the tract. Biondo (1953) on the other hand believed that the meal may spend two or three days in the intestine alone, although it must be stated that his technique is, in the opinion of Castle, open to criticism.

In another paper Castle (1956b) considers the influence of age on the passage of markers through the tract as a whole. Four kids were examined periodically between the ages of one and fifteen months. Her results indicate that the rate of passage was considerably slower in the youngest animals but speeded up somewhat until the time of weaning, after which it was almost constant. Biondo is once more at variance with this conclusion, believing that excretion is more rapid in the younger animals. A few scattered pieces of information can be extracted from the various radiological accounts but where a comparison is possible it will rarely be found that the authorities are in agreement: for example, Sporri & Asher (1940) stated that the large bowel is traversed in 4-4½ hours but Hagemeier (1937) quoted an average of 9 hours for the same event. The circumstances and the ages of their respective subjects were admittedly not identical but even so the discrepancy is wide and not easily explained.

It is thus impossible to deduce much in the way of a conclusion from these results and this being so there can hardly be much advantage seeking to establish a parallel with the occurrences in other species. And indeed except for man most other species are no better documented than the goat. On the basis of two isolated examinations Alexander and Benzie (1951) reported that the passage through the stomach and small bowel was more rapid in the weaned than in the suckling foal but that the contrary is true of the passage through the large bowel, a result in general agreement with our own.

The conditions in the human infant are so dissimilar that it may be doubted whether a comparison possesses any validity.

General Discussion.

Among the first objects of this investigation was the comparison of the impressions of abdominal topography gained from the radiographic study of the living animal with those supplied by the traditional methods of anatomical enquiry. The descriptions of the individual organs have already been given and a general assessment of the results may now be attempted.

In the introduction reference was made to the concept of Fluid Anatomy and the opinion was expressed that the relevance of this approach to the study of the viscera was unwisely neglected in the veterinary field. It is considered that the observations recorded here amply support this view and justify the conclusion that preoccupation with the dead leads to as complete a misconception of the true nature of the visceral anatomy of the ruminant as of man (e.g. Hasselwander, 1921: Barclay 1934, 1936: Tchaperoff, 1939). If any doubt remain on this point a further glance at any of the radiographic series will surely confirm the impossibility of defining in exact terms the anatomy of organs which are constantly in movement and endlessly altering their form, their position and their relationships, and whose size depends on the amount of the ingesta they contain.

It is not, of course, suggested that the radiographic method is the only approach to the study of the anatomy and topography of the viscera: its scope is limited and it possesses certain defects which have already been examined (page 17 et seq.) and of which further consideration would be superfluous at this stage. It is likely that the significance of the objections to this approach to anatomical study can easily be overestimated for the salient point that emerges from this and similar studies is that much of the anatomy of the abdomen can only be expressed in approximate terms: acceptance of this principle explains, and it is hoped justifies, the lack of detail in this account. Nothing would of course be easier than to select for each organ, and for each stage of growth, a single radiograph that depicts its form clearly and to describe this in detail with precise reference to the landmarks of the skeleton. But to what purpose if a second radiograph obtained but a few minutes or even seconds later indicates a quite different configuration? If the comparison is made the precision of the first account is immediately seen to be spurious and the amassing of detail far from augmenting its accuracy merely serves to detract from its reliability.

It would be an overstatement of the case to suggest that the anatomy of the dead has no relevance to the conditions in vivo. So far as the goat is concerned it has been found that the appearances of carefully preserved cadavera fall within the range of the variations encountered in life and it has been possible to match any particular dissection with a radiograph selected from the many available. The defect of the orthodox method lies not in positive error but in omission, for these dissections naturally conveyed no hint of the mercurial behaviour that distinguished the living viscera. It is particularly unfortunate that the relative regularity of the dead specimen conceals this truth, for it is the regularity assumed by the dying viscera and preserved by careful fixing which explains the common tendency of the text books to suggest that there is one normal configuration for each organ instead of a host of equally 'correct' possibilities. This concept of stereotyped uniformity is acceptable only if Anatomy is regarded, in Müller's phrase, "als ein abgeschlossenes Wissengebiet"; but if, on the contrary, it is studied in relation to the living animal, in the exercise of its normal functions, and for its value in the diagnosis and treatment of disease then there is nothing more misleading than this belief. Dogmatic statements of form and position have no place in the description of the viscera. If it is accepted that the dead animal exhibits but a single phase of a scene which in life is constantly changing and if this relationship is borne in mind, it is permissible to compare and combine the results supplied by radiological and orthodox anatomical studies. A general collation of the observations made in the older kids with the conclusions of Wilkens (1956b), whose account of the anatomy of the abdominal topography of the goat appears to be the best available, has been undertaken but as nothing has arisen from the comparison that requires special comment a point by point enumeration of the correspondences may be omitted as it would be as tedious as it is unnecessary.

It is more important to consider briefly the postnatal changes in abdominal topography and in particular the development of the stomach. The foetal development of this organ and the formation of the several chambers by outgrowths from the originally simple tube are matters that cannot be considered here: they have been described on very many occasions and reference may be made to the work of Pernkopf (1931) for a very detailed consideration of the subject, and to that of Schummer (1933) which is especially valuable on questions of prenatal topography. The postnatal development of the stomach of the ox and sheep has been studied by several workers but Tamate (1957a) gives the only account of the changes in the goat: he examined the fresh carcases of 31 kids between birth and the age of 70 days and provides many details of topography. In general his conclusions agree with those reached here and the details need not be considered further since, for the reasons now familiar, too much significance should not be attached to them. He believes that the rumen greatly expands immediately after birth and occupies most of the left half of the abdomen by the age of 25 days. In those animals which were weaned between this age and 30 days he found a further, immediate and very marked increase in the size of this organ and he suggests that approximately adult proportions are reached by 40-67 days, an age rather younger than that suggested here (8-12 weeks). He also noted the tardy development of the omasum and believed that it had grown very little by 68 days, the age of the oldest of the control kids examined in his study. (Consideration of those kids reared upon an exclusively milk diet is deferred).

An exact topographical study in the embalmed calf was undertaken by Lagerlof (1929) and, as would be expected he reached conclusions very similar to those reported here. The rate of development was less rapid in the larger species which matures more slowly and attanment of the adult configuration was delayed until approximately nine months. Development also appears to be steadier in the calf and a sudden rapid expansion of the rumen, on the lines described by Tamate, was not recognised. Comparison of the growth of the omasum is difficult since this organ never attains in the goat a size comparable to that which it reaches in cattle, and in the latter animal its extent at three months already exceeded that of the adult goat. In all species the behaviour of the abomasum and gut and liver is very similar.

There are a number of additional studies of gastric development in which a quantitive estimate of the changes has been attempted and while the methods employed appear to be of very doubtful propriety these papers cannot be entirely ignored in view of the general paucity of literature on the subject and the prominence given to their conclusions in the anatomical texts. The principal results of these studies are collected in Table II, page 210.

Of the papers quoted (Schmaltz (1894) Auernheimer (1909) and Tamate (1957b)) the last may be considered in rather greater detail since it indicates very clearly the doubtful value of such quantitative estimates. Tamate employed the technique usual in these investigations, emptying the various chambers of their normal content before filling them with water in order to measure their volumes. Since he assumes that the figures he obtains represent the natural capacities of these organs attention may be directed in the first place to but a single animal, kid 018, aged 64 days. The body weight of this kid is given as 5 kg and he is satisfied to record the capacity of the rumen and reticulum as 5500 cc and that of the omasum and abo-

TABLE II Alterations in gastric proportions
(Modified and expanded after Tamate (1957b)

Author	Species	Age and Ratio, Rumen: Abomasum *								
Schmaltz (1894)	Ox				4 wks 1:2	6 wks 2:3	8 wks 3:2		4 mths 4:1	
Auernheimer (1909)	Sheep			3 wks 1:2				3 mths 3.5:1	4 mths 4.4:1	5 mths 5:1
Tamate	Goat	1-4 days 1:4	7-10 days 1:2	16-25 days 1:1.03		5-6 wks 5.7:1	7-8 wks 4.6:1			

* Tamate's figures give the ratio Rumen + Reticulum: Omasum + Abomasum.

masum as 780 cc: the implication, that the stomach when full weighs considerably more than the entire animal, is obviously absurd. Other figures are little less unreal and the suggestion that they have an absolute value may be dismissed without further argument. It is less easy to decide whether or not such estimates of capacity express the relative proportions: it seems unlikely that they do, for almost certainly questions of temperature, ante mortem tone and engorgement, and post mortem delay influence the results to an incalculable and variable degree. The only conclusions permissible from the examination of his figure are those correlating, in a general way, the enlargement of the rumen and reticulum after weaning with the increasing body weight and the relative slowing of the rate of abomasal development - conclusions evident to the naked eye. Enough has been published elsewhere (Alvarez (1948) and Smith (1951) may be consulted for references to the literature) for it to be abundantly clear that the dimensions and capacities of hollow organs are not susceptible of measurement and it is surely preferable to accept this conclusion than to seek to suggest a false accuracy by mensuration. If exact records are really necessary then at least weights are unambiguous and may show whether there is growth of the tissues of which the organs are composed; naturally they cannot provide an absolute indication of the size of the organ, since such a conception has no real meaning.

Postnatal changes in the form, proportions and location of the viscera are not of course peculiar to the ruminants although they are perhaps especially obvious in these animals. Relatively extensive alterations in the human viscera occur during infancy and early childhood and have been described in detail (e.g. by several contributors in Peters, Wetzel & Friedrich, 1938): similar changes are known to exist in other species, e.g. the dog (Meyer) and horse (personal observations, manuscript in preparation) but there is a great lack of literature on this subject. Presumably such alterations occur in all species and continue the differential growth of prenatal life and it seems reasonable to expect that the changes will be more marked in herbivorous than in carnivorous animals since not only do these possess alimentary tracts of considerably greater complexity, but chemical and physical differences between the milk diet of the sucking animal and the pabulum of the adult are greatest in these animals. This expectation is in accordance with what is known of the few species already mentioned but information regarding the changes in a wider range of subjects is urgently required. In particular a study of the postnatal development of the stomach in other forms, such as the colobid monkeys or the kangaroos (Pernkopf, 1937), in which this viscus is of a complex nature would be most valuable.

In considering these matters it is interesting to speculate on the relative importance of genetic and mechanical factors in determining the later morphogenesis of the digestive organs for it is known that while the general course of development is predetermined the rate and extent of the changes are also influenced by the nature and volume of the food. Haesler (1929) has collected a vast amount of information relating to the influence of diet on the development of the alimentary tract and he reports additional experiments of his own which demonstrate the effects of dietary variations on the length, volume, weight and structure of the digestive organs of pigs; of these criteria the last two at least are incontrovertible and show conclusively how important is the variation due to this cause. Similar experiments on other species are recorded by Mangold and Haesler (1930) and many others. Trautmann (1932) appears to have been the first to study these matters in the ruminant and he demonstrated that in kids reared exclusively upon milk the first two chambers show comparatively normal development. 'Die allgemein verbreitete Annahme, dass die eigentliche strukturelle vollkommenheit des Pansens und der Haube erst nach Aufnahme von Rauhfutter erreicht wird, ist nicht richtig". The conclusion, and it was based on animals reared to 7 months, was unexpected but perhaps can be partially explained by the activity and thus the exercise of the muscle of the walls of these two organs, which is now known to take place in the sucking period.

The omasum on the other hand, shows very little development in the absence of the stimulus provided by the introduction of roughage and this may be correlated with the absence of a mechanical function or activity of this part when the ingesta are purely fluid. The effects of the mechanical stimulus could be seen once solid food was provided for a doubling of its size was brought about within the week. Trautmann, who also notes the histological effects of the different diets, gives no weights or measurements to indicate the progress of development but his findings are most convincingly supported by a series of photographs of the postmortem specimens.

Blaxter, Hutcheson, Robertson and Wilson (1952) conducted a very similar experiment with calves and they found that the roughage stretched the walls of the first three chambers without, however, there being a corresponding increase in the weight of the organs compared with those recorded for the unweaned controls. This is a further indication of the general invalidity of the work of Tamate to which reference has already been made. Tamate believed that there was an actual growth of the rumen which was accelerated by weaning and he implied, without putting the matter clearly, that there was an increase in the tissue of which the organ is composed: the corollary which he also reported, namely that there is a decrease, absolute and not relative, in the abomasum on weaning is alone sufficient to cast doubt on the justification of making such a conclusion solely on the basis of the capacities.

It was intended to include a similar investigation in the present study but as has already been indicated the animals set aside for this purpose succumbed to disease before any intensive study of them was made. Preliminary results on only two subjects, and these diseased, indicated that at three months the ruminoreticulum sac of the milk-fed animal occupied a proportion of the abdomen similar to that seen in controls of four or five weeks. More important however was the effect on the mechanics of the tract, for as yet this aspect is unreported in the literature: it seems that in these milk-fed kids the abomasum retains its juvenile vigour and continues to show a predominantly systolic type of activity. Rumenoreticular contraction and spasmodic rumination also occurred in these subjects, and it may be emphasised in these animals alone there was a reflex of the abomasal contents into the first chambers in the fashion related by Akssenowa (1932) and Trautmann & Schmitt (1933).

It is obviously necessary to repeat this part of the investigation on a much more extensive scale and this it is hoped to do on a future occasion.

The matter is of some importance for the post-natal growth of the stomachs of the ruminant is not merely of academic interest but possesses considerable significance for the stock raiser. The appreciation that the forechambers are active soon after birth and that they will freely enlarge to accommodate fodder has led to the formulation of new systems of rearing in which the calves are precociously introduced to solid foodstuffs. It appears that animals treated in this way are well able to digest appropriate rations and that they show an early and unusually rapid growth, accompanied by an increase in gastric capacity (Dow, personal communication, 1956). According to this authority there appears to be a real growth of the stomach accompanied by an increase in the thickness of the wall and by the differentiation of the mucosal linings to resist the abrasive effect of the harsh ingesta. This experience appears to contradict the findings of Blaxter and his colleagues but it will be recalled that in the latter experiments the comparison was made between calves reared in the traditional way and those in which the introduction of solids was delayed: it might be presumed therefore that the normal development of the muscle and mucosa proceeds regardless of the stimuli of exercise and friction but that unusually pronounced stimuli provoke an additional reaction. But more exact studies are necessary before a final verdict can be given. Certainly it is becoming increasingly evident that both the anatomy and the activity of the digestive organs of the young ruminant are much more precociously developed than was formerly recognised.

Sufficient has been said concerning the various activities of each part to render further discussion of the individual processes unnecessary. A few remarks of a more general nature may be permitted in conclusion in order to stress the great diversity of behaviour which has characterised almost every visceral function which has been examined in this study: there is hardly one event, however simple which is always completed in the same way, and where the activities are more complex the diversity increases in proportion. Thus while it is easy to recognise an average behaviour for each part it is hardly possible to define the normal in terms sufficiently comprehensive to include all the varieties of activity seen in the healthy goats and yet sufficiently definite to be genuinely descriptive and it is evident that a revised conception of what is meant by the use of the term 'normality' in relation to the anatomy and mechanics of the digestive tract is indicated.

It is certain that much remains to be learnt of almost every aspect of the mechanics of the ruminant alimentary tract, and of the stomach in particular, and this need occasion no surprise if attention is directed to the discoveries that are even now, after sixty years of intensive study, being made concerning the human organs. Indeed it may be doubted whether a full appreciation of the normal range of appearance and activity of the ruminant organs will ever be gained unless there should appear a clinical stimulus to the radiological study of these parts - and of this there is at present no sign. Repeated investigations will however gradually remove some of the uncertainties.

It is hoped that the present study may have helped to elucidate some points, particularly in connexion with the mechanism of the omasum and of the abomasum, and that it has demonstrated the activity of the latter organ more exactly than hitherto; that it has cast much light upon the activities of the other chambers of the stomach cannot be claimed - indeed the reverse is true and what was formerly precise and clear cut has now, in the writer's mind at least, acquired a new uncertainty. Various points in the description of the other organs may possess some novelty and some events, themselves by no means novel, may have received a not unwelcome objective confirmation in the serial radiographs.

Undoubtedly, however, the most important outcome of such a study as this is the additional proof it supplies of the integration of the anatomy and function of the viscera and the demonstration that any consideration of either of these aspects in isolation, and without regard to the other discipline, is sterile and must assuredly fail in its purpose.

Summary

The anatomy and motor activities of the digestive organs were studied in fifty-two goats, aged between sixty hours and fourteen months. The animals were hand-reared and although provided with access to solid fodder from the first, continued to be fed a limited amount of milk beyond the usual time of weaning. The abdomen was dissected in ten animals embalmed in the standing position but, this apart, radiological methods were employed. In addition to single films, the movements were studied fluoroscopically and by serial radiography, great reliance being placed upon the latter as supplying an objective record. A number of cinefluoroscopic sequences were also obtained.

The radiological anatomy and the post-natal changes in topography are described and the details cannot conveniently be summarized. Development is rapid especially in the first six weeks and a virtually adult condition is reached by three months or thereabouts. The following are the principal observations on mechanics.

On deglutition, fluids may be temporarily arrested at three points en route to the stomach and may pass to and fro in the thorax before passing the cardia.

The rumen and reticulum develop rapidly after birth, especially between the second and sixth weeks. Both are active from the first weeks and an adult pattern of behaviour appears soon after the sixth week. The ruminoreticular activity never acquires

great regularity and, in addition to the two-stage reticular and the two- or four-stage ruminal cycles commonly described, shows additional independant contractions of the major and blind sacs.

Growth of the omasum is retarded until considerable amounts of solid fodder are consumed. Its main activity is co-ordinated with reticular contraction when the upper pole dilates and fills: later this part contracts and the expulsion of food is assisted by constriction of the middle and distal sections. Alternating contractions and relaxations occur at other times also.

The abomasum determines the abdominal topography at birth but soon decreases in relative size. Its parts and activities resemble those of the simple stomach and both uninterrupted peristalsis and antral systole occur: the latter is regarded as a modification of the former and predominates during the first six weeks or so: later the movements are almost exclusively peristaltic. Activity is [redacted] greatest between the second and sixth week.

The duodenal bulb exhibits systolic and other less clearly defined contractions. The remainder of the small intestine shows peristaltic, segmental and other activities in complex combination. Peristalsis predominates in the proximal, more active, part and gradually gives way to segmental activities when the intestine is traced distally.

The large bowel continues the gradient of activity. The caecum and colon show peristaltic and (proximally) antiperistaltic contractions in addition to several types of segmental contraction.

The results as a whole emphasise the precocious development of adult topography and behaviour and demonstrate the close integration of structure and function. It is suggested that the exclusive study of the dead animal leads to a misconception of the essential nature of visceral anatomy.

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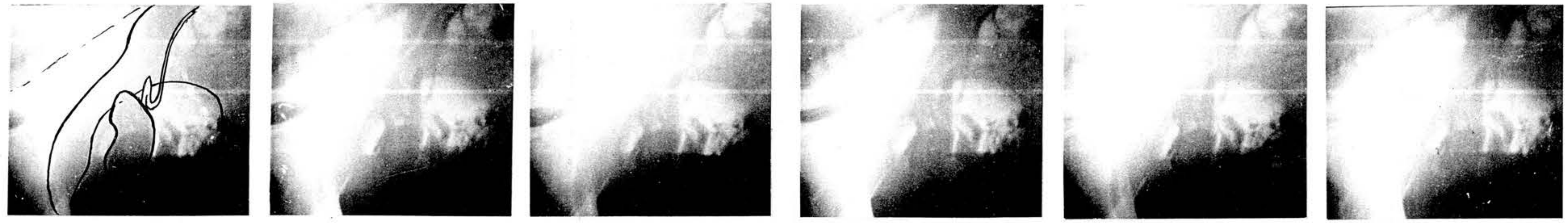

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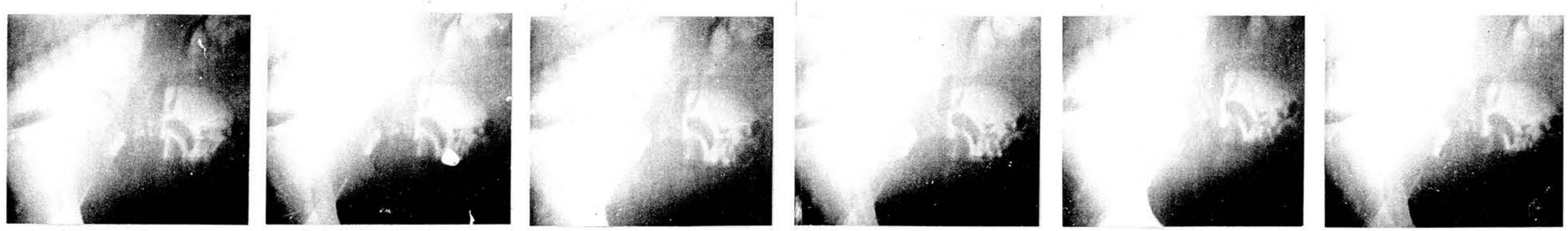

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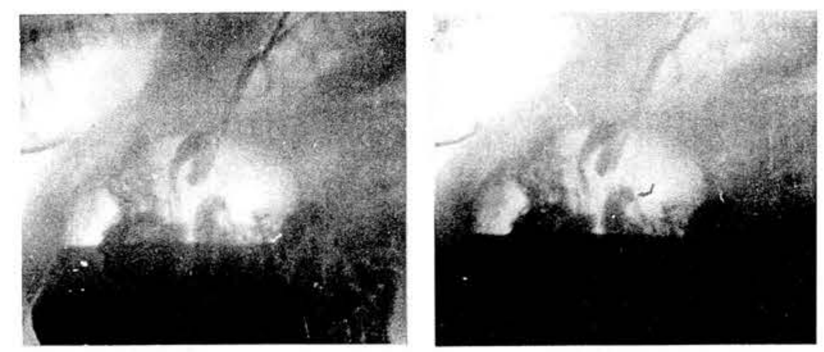

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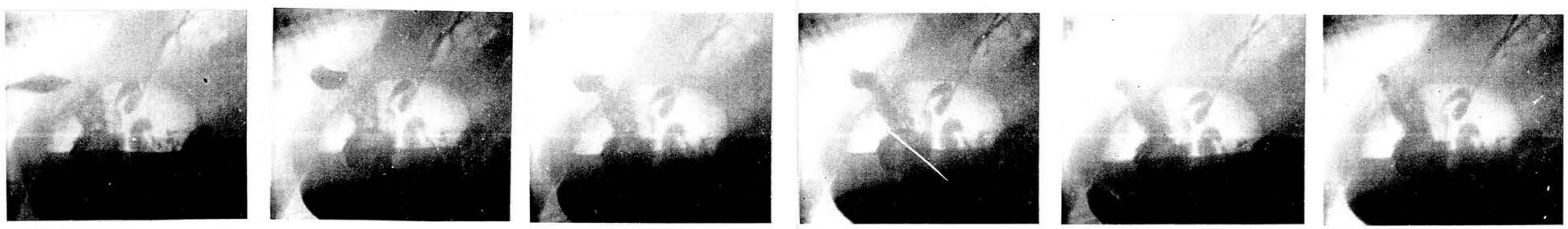

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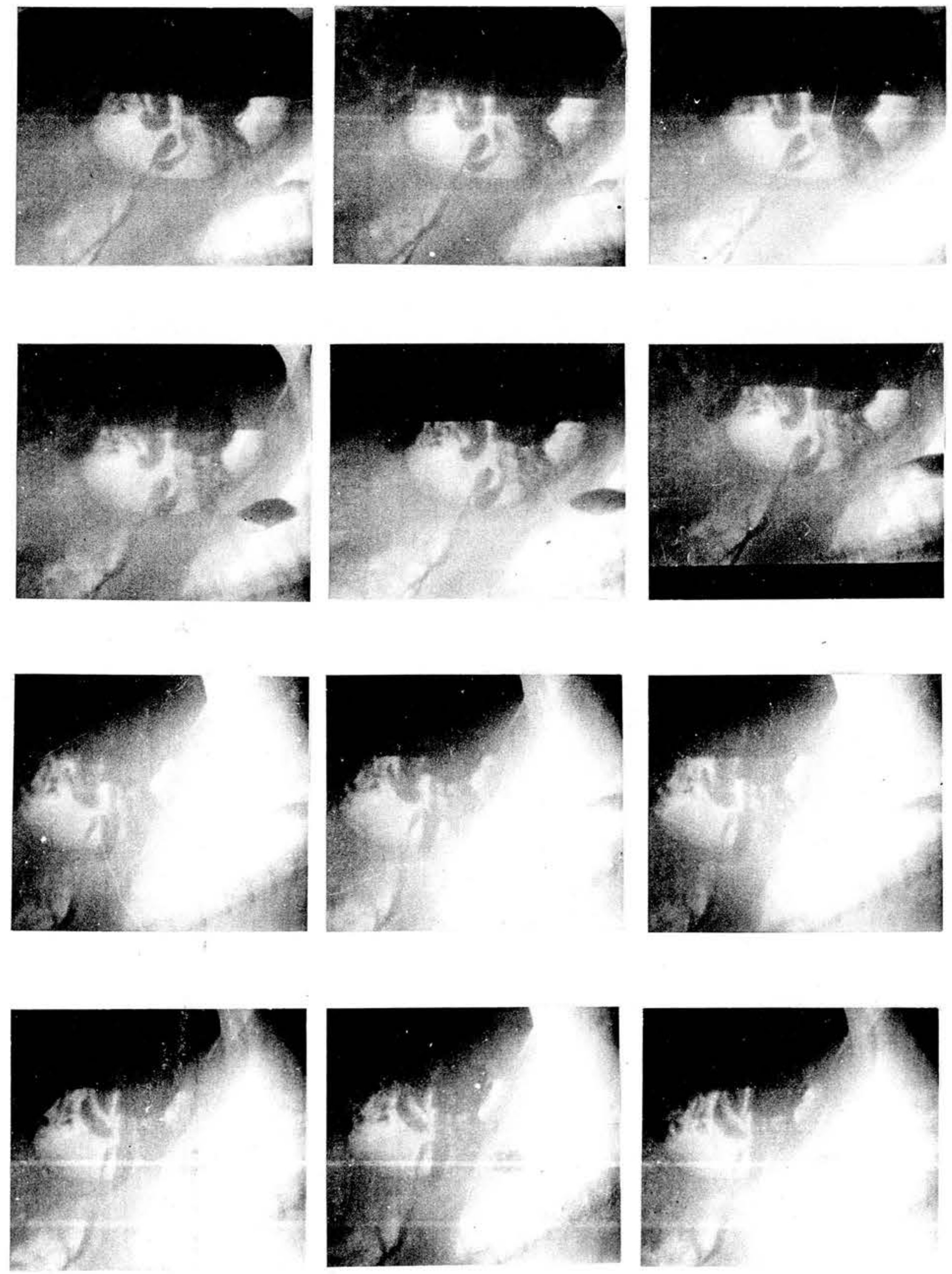


Plate 1.

Figure 8. The entry of milk into the abomasum.

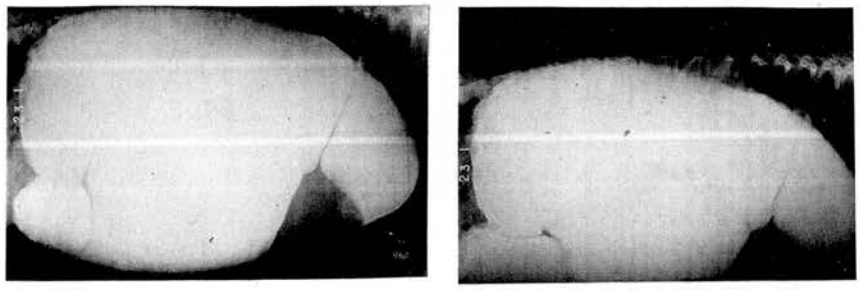
These frames are taken from a cine-fluoroscopic sequence which was exposed at the rate of 12½ frames/second. The extract covers a period of almost four seconds of which one second is omitted since movement at the time was minimal. The subject was aged fifteen weeks.

The quality of the pictures is poor since the exposure represents a compromise between that appropriate for the portrayal of the thoracic organs with one more suited to the study of the abdomen. In the first frame the diaphragm, vertebral border, omasum, abomasum and the second part of the duodenum have been outlined. The distal part of the abomasum and the origin of the duodenum overlie the abomasal gas but their exact delineation is difficult. A quantity of the opaque milk feed lies in the oesophagus at the left margin of the picture.

The approaching column of fluid has a fusiform 'head' which opens up the oesophagus in advance of the main mass. As it passes behind the heart the shadow thins and it breaks into two fragments of which the anterior runs forwards out of view while the other continues to the level of the diaphragm where it is halted and whence it runs back to join the main mass, leaving a thin layer of material in the caudal section of the oesophagus. A small part flows into the stomach (frame 10). There is little movement for a time and then gradually the milk trickles through to collect once more before the cardia where it reforms as a mass with a short fusiform outline (e.g. frame 38). When the entry to the stomach is opened this collection seems to be compressed from behind and it proceeds through a short constriction, probably corresponding to the level of the diaphragmatic crura (e.g. frame 40), which is continued caudoventrally as a rather wider segment which represents the oesophageal groove (e.g. frame 42). The lower end of this shadow overlies the omasum and the exact location of the reticulo-omasal orifice cannot be determined. It will be observed that in its passage through the omasum the milk appears to be confined to the anterior border wherein lies the channel or sulcus omasi. It is not possible to see the exit from this chamber into the abomasum as the lower pole of the third stomach is obscured throughout the series.

The trace of milk in the oesophagus seen in the last three frames represents the arrival of a further gout.

The animal did not remain immobile during the exposure and its movement conceals a respiratory excursion of the diaphragm. It will be observed that one consequence of the diaphragmatic movement is an alteration in the disposition and inclination of the duodenum. Some movement and transport at the portal flexure of this organ will also be discerned.



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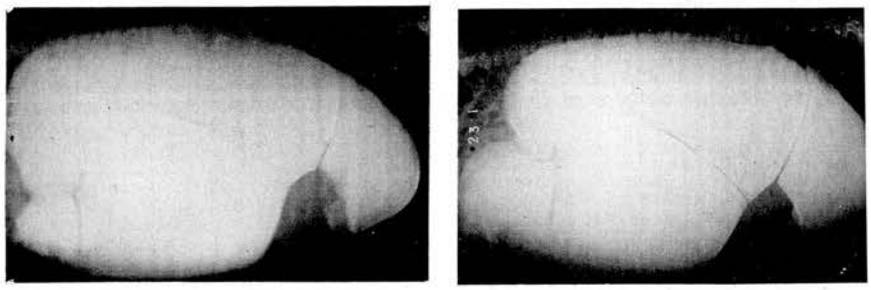

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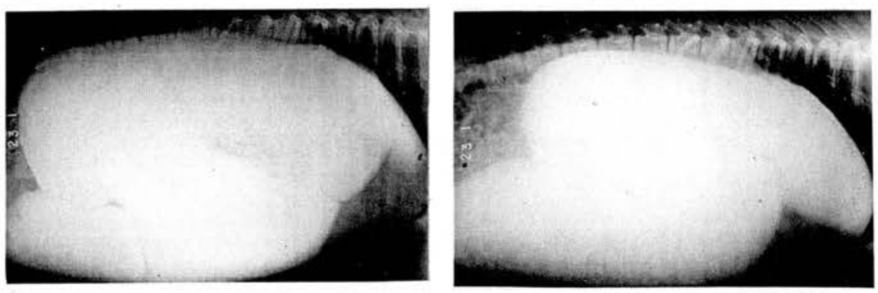

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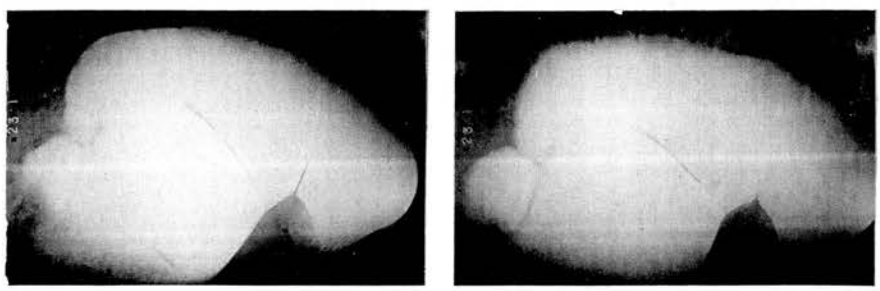

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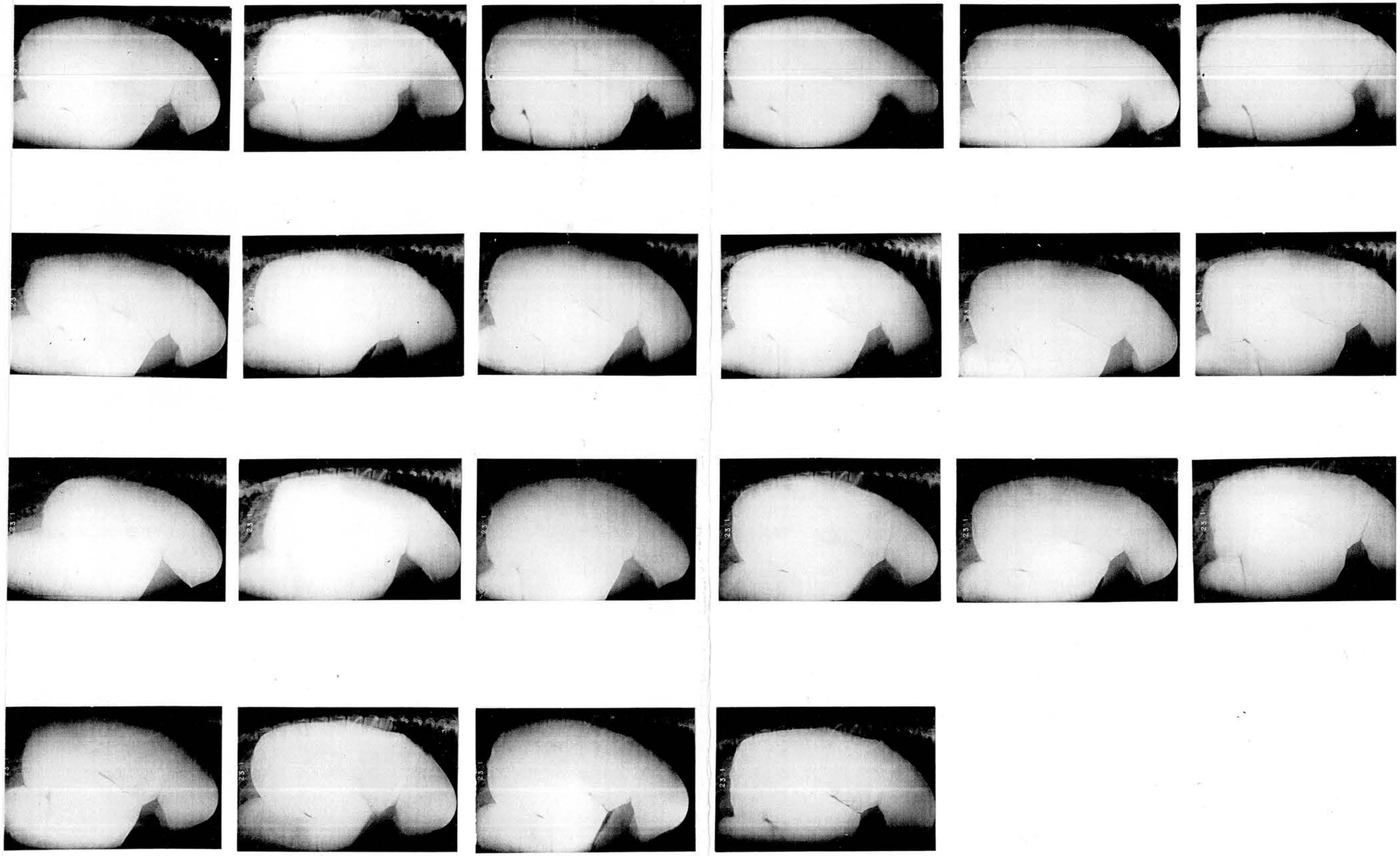

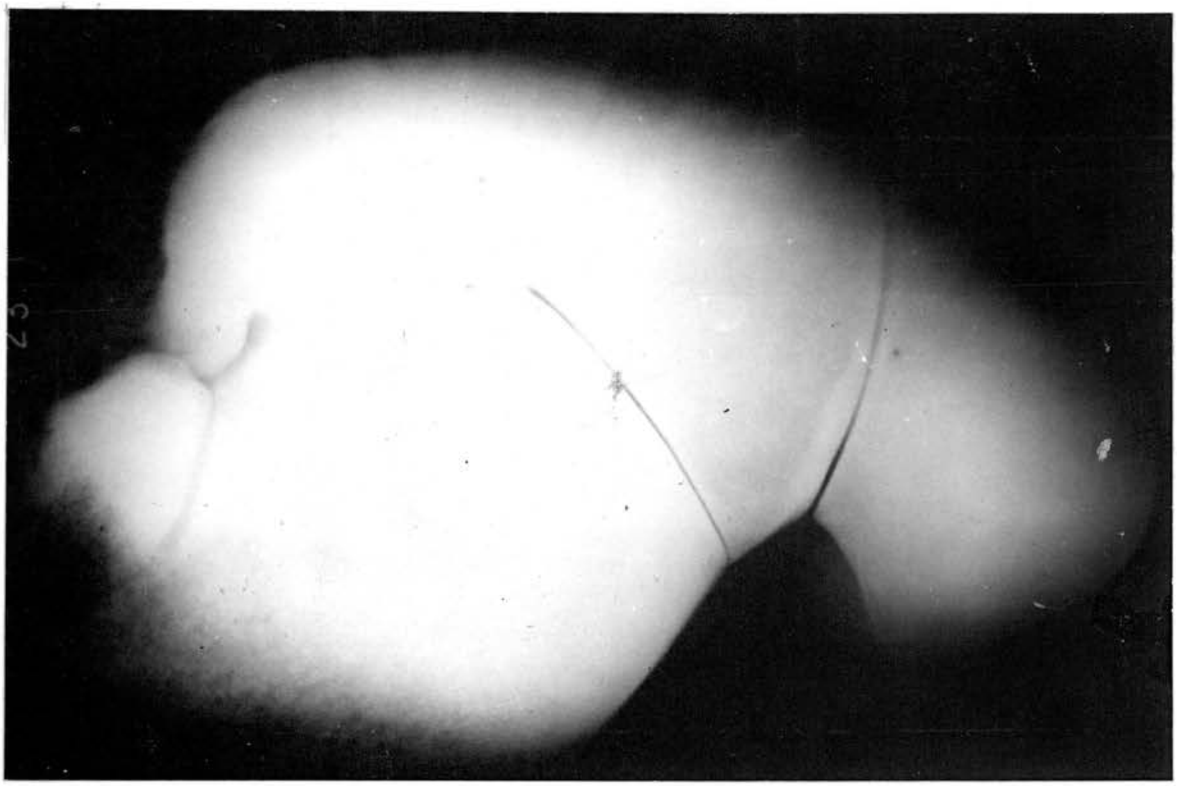

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Plate 2.

Figure 32. Ruminoreticular contractions.

The subject was aged nine weeks and the series was obtained fifteen minutes after the administration by stomach tube of an aqueous suspension of barium sulphate. The series consists of 30 frames which were exposed at two second intervals, the sequence taking exactly 60 seconds. Each exposure lasted 0.5 seconds and some movement is apparent in certain frames. Since this series is the principal record presented of the contractions of the rumen and reticulum it may be examined in some detail: for this purpose a frame by frame analysis is most convenient.

Frame 1. The reticulum is relaxed and its posterior margin is indented to conform with the abomasum: it is separated from the atrium by a clearly defined division corresponding to the rumino-reticular fold. The dorsal sac of the rumen extends to the lumbo-sacral junction and the dorsal blind sac hangs downwards over the corresponding ventral part. The anterior and posterior pillars are so directed that the dorsal sac is crescentic in outline: the anterior pillar is the more prominent of the two and extends considerably towards the roof and posterior extremity of the rumen.

The ventral blind sac is contracted and the coronary pillar which marks its extent is well defined.

Frame 2. The film was badly placed and the ventral part of the rumen is lost to view. The dorsal sac has relaxed somewhat and the ventral sac contracted: the ventral blind sac has enlarged to two or three times its former dimensions.

Frame 3. The changes evident in the previous frame have continued and the relaxation of the dorsal blind sac is also conspicuous.

Frame 4. A reversal of the contractions is now apparent and the dorsal sac and the two blind sacs have become smaller, the ventral sac larger. Contraction of the ventral blind sac brings its coronary pillar more clearly into sight. Expansion of the ventral sac results in a filling out of the lower part of the anterior border of the rumen.

Frame 5. The dorsal blind sac has begun to expand once more but the ventral blind sac is even more reduced in size. The atrium is somewhat relaxed, the reticulum contracted and possibly this frame and its immediate successor record a rapid reticular contraction. (The series was in fact timed to commence some 5 seconds before such an event but the evidence of its occurrence is equivocal).

Frame 6. The reticulum, which is reduced in size, is seen in movement and is probably relaxing since the atrium is contracted from its previous form. The main ventral sac is also contracted and the other parts of the rumen are relaxed.

Frame 7. The reticulum and atrium are both enlarged but the other parts show little change.

Frame 8. There is now an expansion of the ventral sac and contraction of the blind sacs. The pattern of the reticular cells is apparent on close inspection.

Frame 9. The reticulum and ventral sac are further relaxed while the other parts contract.

Frame 10. The reticulum and atrium are greatly relaxed and the pillars very evident. Both the main division and the diverticulum of the dorsal sac are greatly contracted while the ventral parts are much relaxed.

Frame 11. The expansion of the ventral blind sac appears to continue but the movements of the other parts of the rumen are reversed.

Frame 12. The ventral sac is reduced to very small bulk while all the other divisions of the two chambers are enlarged. The ventral blind sac is especially dilated.

Frames 13-16. The process begins to be reversed and for a spell there is little movement. Towards the end of this period of relative quiescence the reticulum begins to reduce in size.

Frame 17. The reticulum is greatly contracted and its contents have been ejected into the very much enlarged atrium. The ventral sac is somewhat flattened and extends further forward but otherwise the rumen shows little change.

Frame 18. The reticulum is much enlarged and is still expanding. The atrium is contracted and is very small and the entire dorsal half of the rumen is diminished in all dimensions. The ventral parts are in diastole.

The change from the previous frame is very marked.

Frame 19. Full relaxation of the reticulum. The atrium has begun to relax but the other dorsal parts, and in particular the dorsal blind sac are still tightly contracted. The main ventral sac is somewhat reduced.

Frame 20. There is some decrease in the size of the reticulum. The dorsal sac has enlarged especially in its blind sac, but the ventral blind sac is further contracted.

Frame 21. These changes continue.

Frame 22. Now the dorsal parts are much enlarged and while the ventral sac is greatly contracted its blind sac is relaxed.

Frame 23. An expansion of the reticulum and of the ventral sac and a slight contraction of the ventral blind sac are the changes most in evidence.

Frame 24. An enormous increase in the size of the ventral sac with a reduction of all the other parts of the rumen have occurred.

Frame 25. Since the last frame there has been a very great increase in the size of the reticulum and a less marked enlargement of the ventral sac. The anterior pillar is very oblique and the atrium quite large, but the other parts of the dorsal half of the rumen are contracted almost to the point of disappearance. The ventral blind sac is also much reduced. The anterior and posterior pillars converge dorsally.

Frame 26. The reticulum is even more relaxed. The various dorsal divisions have commenced to expand, this being particularly noticeable for the atrium. The ventral blind sac also shows some increase.

Frame 27. The ventral sac is considerably, the reticulum less markedly, reduced while the remaining parts expand.

Frame 28. The ventral sac is in full systole. The dorsal sac and the two blind sacs are much enlarged.

Frame 29. A continuation of the same changes may be recognised.

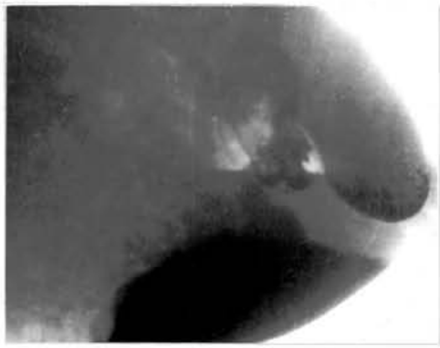
Frame 30. The ventral sac relaxes once more, while the other parts, particularly the dorsal blind sac, contract.

It will be evident from the serial films and from the foregoing description that the sequence of contractions is not easily characterised in few words. The relationship of the activities of the blind sacs to those of the main cavities with which they are associated is especially confusing. For example the activity of the ventral blind sac is generally - but not always - the opposite of that involving the main ventral sac: and while the two blind sacs often contract together their activities at other times are reciprocal. It appears unlikely in fact that there is a general and inflexible rule governing the movements of the various ruminal divisions. The general cycle of activities of the reticulum and the atrium, and of the principal dorsal and ventral compartments is however indisputable.

It will not have escaped notice that the relative proportions of the various parts are almost constantly altering and that the only period of even approximate quiescence preceded the reticulum contraction shown in frame 17. This is a common observation and it accords with the belief that a refractory period precedes reticular contraction (Brunaud & Dussardier, 1953a): it is not however a constant occurrence.

Before the series was exposed the reticulum exhibited a fairly regular rhythm with contractions recurring every 50-55 seconds and the series was timed to commence a few seconds before one of these. Unhappily it does not appear to have been successful in this aim although possibly the reticular changes shown in frames 6 and 7 represent the anticipated contraction. It seems more likely however that the attempt at contraction was abortive and this interpretation is in better accord with the occurrence of a full contraction only 20 seconds later.

A faint hint of an omasal shadow in certain frames suggests that some of the agent is already leaving the first two chambers of the stomach.



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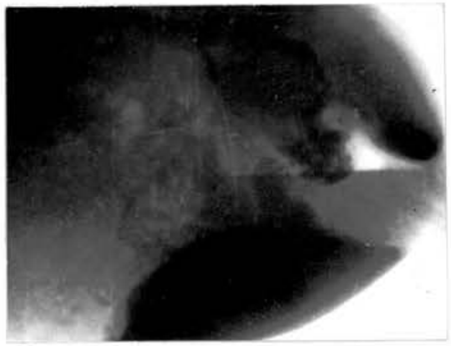

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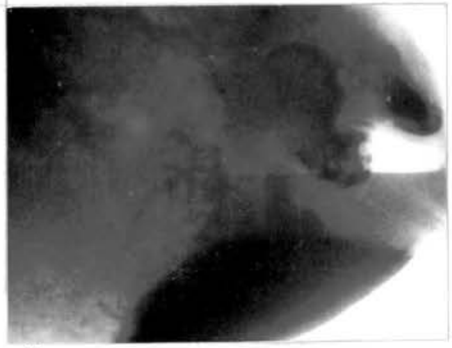

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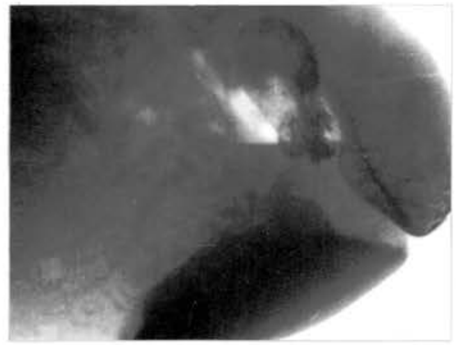

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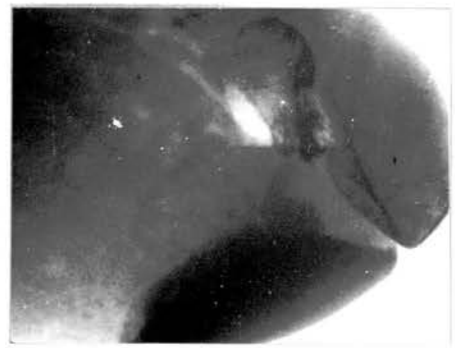

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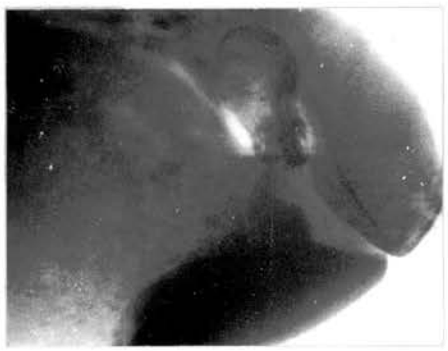

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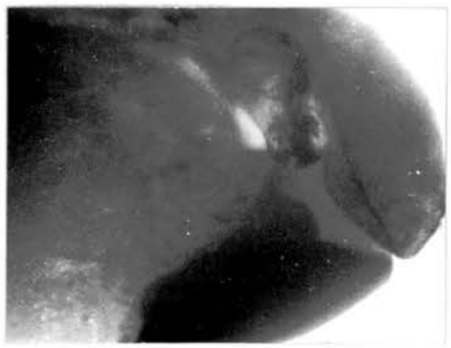

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Plate 3

Figure 33. Reticular contraction with omasal motility.

Exposure of this sequence was initiated immediately the commencement of a reticular contraction was observed on the screen. The film was exposed at 12½ frames/second but only every sixth frame is reproduced. The extract thus covers approximately 7½ seconds.

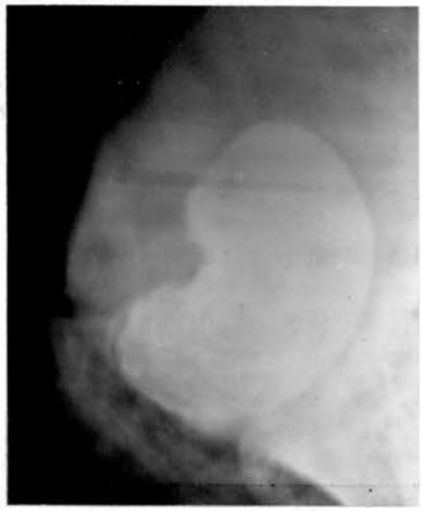
Observe the abomasal gas and overlying this the bean-shaped omasum: low and behind the omasum lies the sinuous outline of the pars pylorica. The early part of the contraction is not recorded but the whole movement may be estimated to take 2½ seconds: the duration of the subsequent relaxation is less easily timed and while the reticulum returns to its former size in 3 seconds, further relaxation may be anticipated although it is not shown here.

On contraction the contour of the reticulum becomes clear and rounded and its shadow deepens: it is just possible to detect the marginal indentations in frame 7. Simultaneously there is a forward and downward movement of the abomasal fundus and the omasum is carried forwards with this and is also bent on itself becoming more regularly bean-shaped: the upper extremity expands (frame 13). As the reticulum relaxes the organs return to their former position while the reticulum once more moulds itself in adaptation to the abomasum. An indentation of the posterior margin helps to separate the lower pole of the omasum (frame 31) and, while the whole organ is elongated, this part may be seen in the following frames to contract somewhat when a small 'spike' of densely contrasted material appears to separate itself from the lower extremity (frames 43 onward), without however becoming detached. Finally there is a general shortening and widening of the omasum and a rotation about its long axis which once more brings the concave outline of the anterior border clearly into view.

The significance of the omasal changes is discussed in the text.

It will be noted that the alteration in the position of the abomasum is not extensive and it is difficult to see that there can be much shifting of its contents into the pars pylorica to stimulate the activities of this part in the manner suggested by Phillipson (1939).

1



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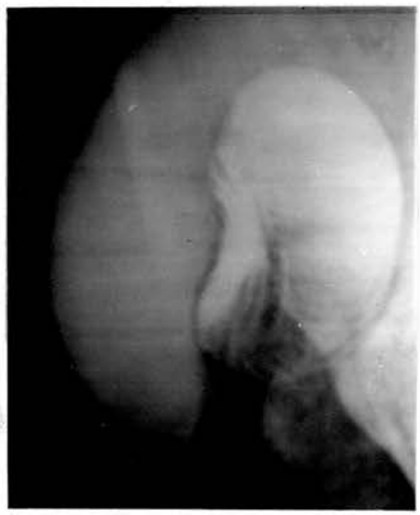

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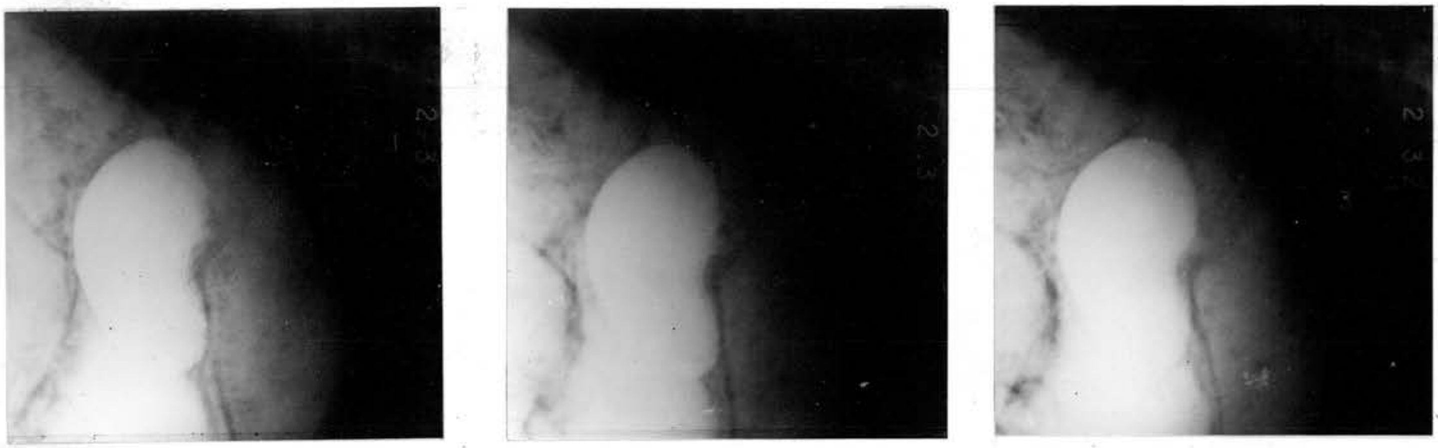
Plate 4.

Figure 34. A reticular contraction.

The subject was aged 9 weeks and the series exposed two hours after the administration by stomach tube of an opaque meal. The interval between exposures was two seconds.

In the first frame the parts of the organs shown are easily identified - atrium ruminis, reticulum, abomasum and omasum. The concentration of the contrast agent along the concave anterior margin indicates the position of the sulcus omasi. The alternation of the leaves and recesses is faintly shown. In the second frame the reticulum is contracted and the abomasum has come up below its fundus: the reticulum is carried forward and upward but much of the change in its shape appears to result from an increased curvature of its long axis. The increase in density suggests that a little material has been drawn in. In the next frame the reticulum has relaxed and the organs have largely reverted to their former position and appearance. Apart from a slight contraction of the reticulum the last frame shows little further change.



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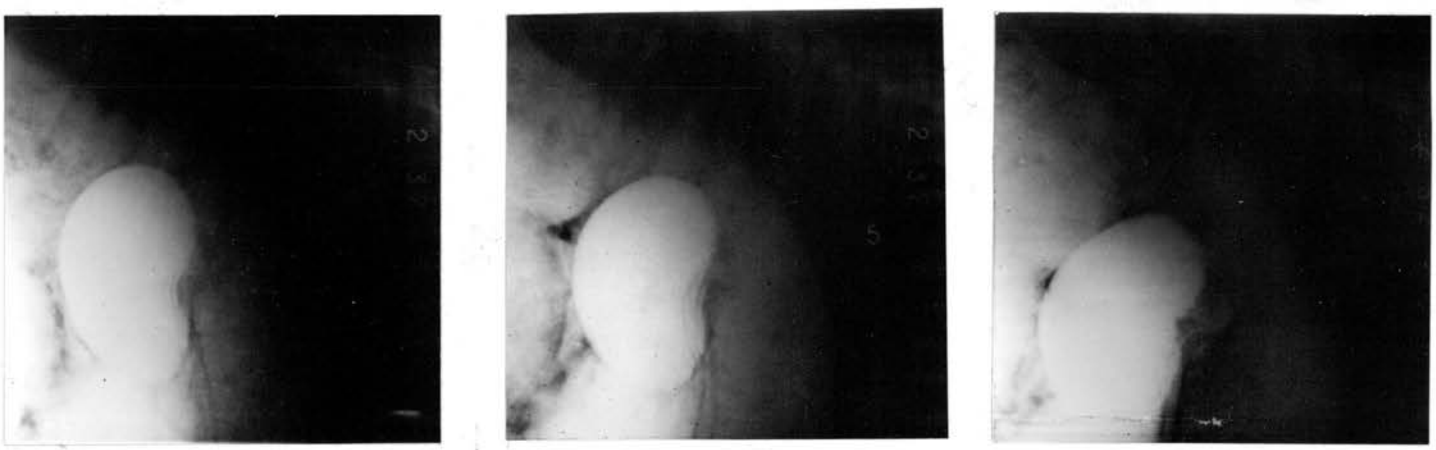

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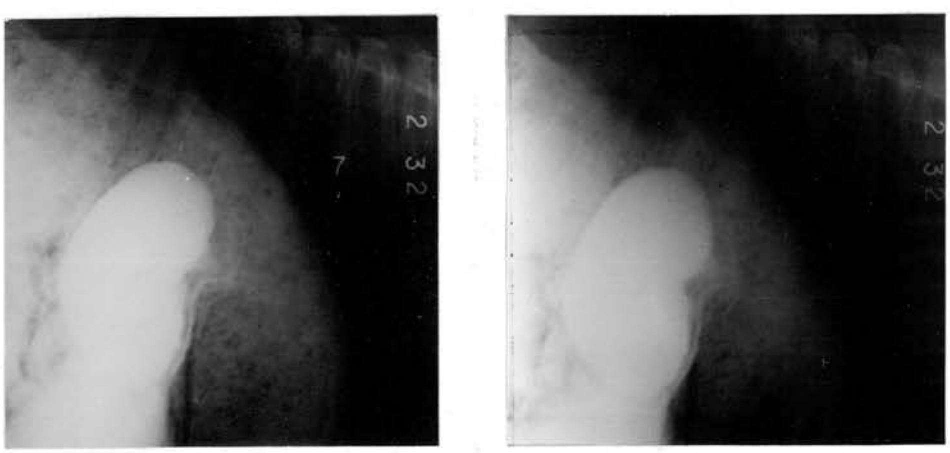

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Plate 5.

Figure 39. Movements of the omasum.

The subject of this series was aged thirteen weeks and the films were obtained one hour after the administration of an aqueous suspension of barium into the rumen. The interval between the frames was $2\frac{3}{4}$ seconds.

Much of the contrast agent appears to have entered the omasum and been deposited here, perhaps by the absorption of the suspending fluid. The omasum is thus clearly outlined in comparison with the rumen and reticulum, the latter organ being very difficult to discern since the films were necessarily over-exposed in order to depict the omasum with clarity. A dense shadow extending from the lower pole of the omasum represents the abomasal body and fundus.

The omasum exhibits certain intrinsic activities during a period when the movements of the other parts were minimal. There is no clear evidence however of the entry of food from the reticulum (which would not be expected) or of its discharge into the abomasum. In the first frame the upper pole of the omasum is relaxed and the lower pole contracted. The indentation of the anterior margin corresponds to the position of the sulcus omasi and certain striations in this region indicate the presence of the omasal leaves. In the next two frames the organ has become slightly more symmetrical. Frame 4 shows a marked shortening and rounding of the organ which is continued in the succeeding film. Here it appears that the organ has rotated somewhat and the anterior curvature is concealed. By the fifth frame the lower part is significantly enlarged beyond the dimensions of the upper pole and this expansion continues while the upper part contracts. At the end of the sequence illustrated the omasum possesses a form very different from that first shown.

It appears highly likely that the alternation of expansions of the upper and lower poles result in the drawing in of food from the reticulum and in forcing it through the omasum. The sequence is visualised thus. The upper pole is expanded when the reticulum contracts and ingesta pass through the reticulo omasal orifice. (This part of the cycle is not shown in the present series: see however fig. 32). This part of the omasum then contracts and the lower part expands and with the closure of the entrance to the organ the food material is drawn distally. Later the lower pole contracts and the contents of this part are passed through the relaxed omaso abomasal orifice into the abomasum. The alteration in the general form of the organ and its assumption of a shortened and more rounded configuration may be responsible for the introduction of the ingesta to the interlaminar recesses. It is not possible to assign a function to, or to determine the effect of, the rotation about the long axis of the organ: this may be a consequence of the muscular contraction but alternatively may be a movement induced by extrinsic activities.


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2


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Plate 6.

Figure 62. Antral systole.

Series:

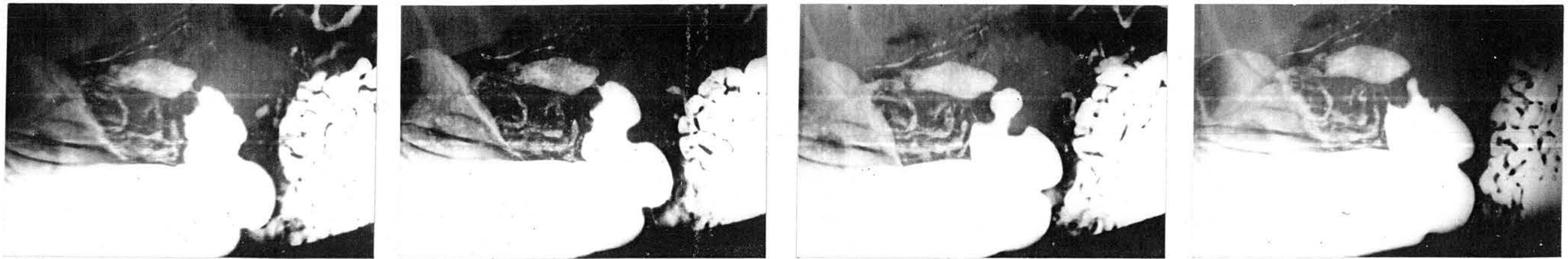
The subject was aged three weeks and the exposure made 1 hour 20 minutes after feeding. Frame interval 2 seconds.

This short run is included to show antral systole at approximately 4/5 natural size.

In the first frame the contraction of the antrum is still at a comparatively early stage and its cavity freely communicate with the remainder of the organ. The indentations of the pars pylorica is conspicuous and the pylorus doubtfully open - probably it is outlined merely by a little material adhering to the mucosa. The next peristaltic wave is clearly visible.

Two seconds later the contraction is much more advanced and the antrum is well separated from the sinus region: the pylorus is open and exit of ingesta may be assumed. A contraction of the duodenum at the apex of the bulb is also visible. In the final picture systole is almost complete and the pylorus is once more closed and indicated by a thread-like connexion with the bulb. The next 'antrum' is well formed and further waves appear on the corpus. The irregularities of the new 'antral' shadow indicate mucosal rugae.

Observe also the slow progress of the chyme through the intestinal loop situated above the pyloric region.



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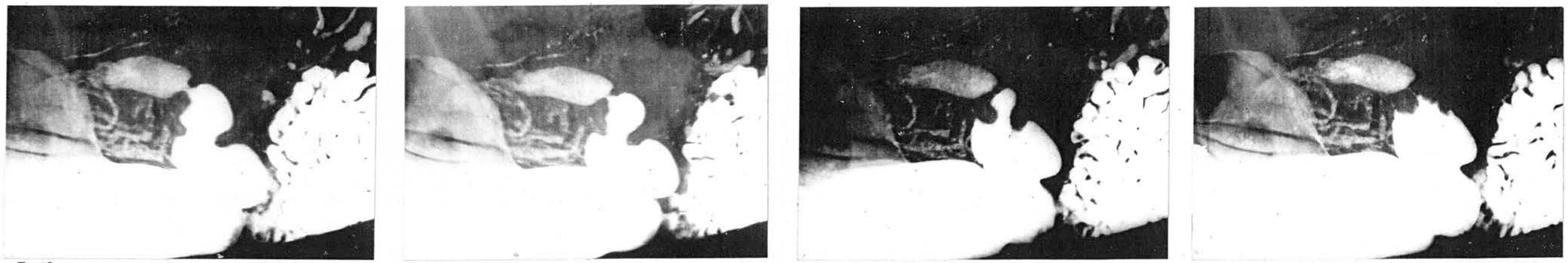

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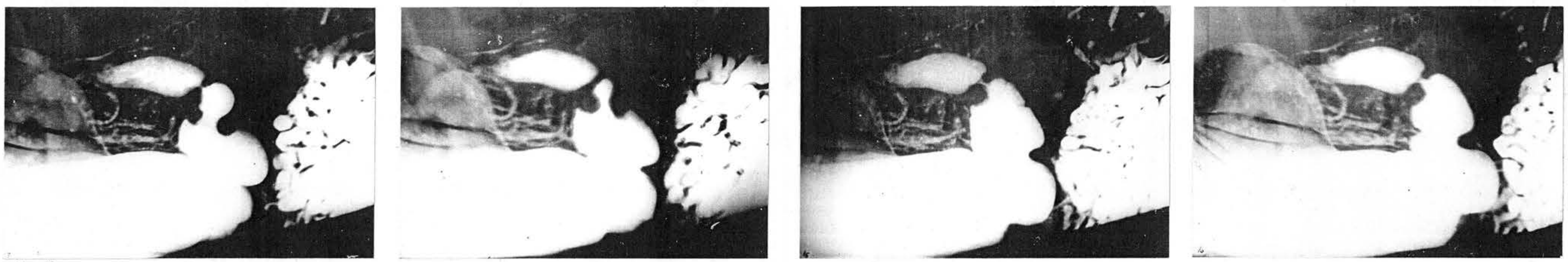

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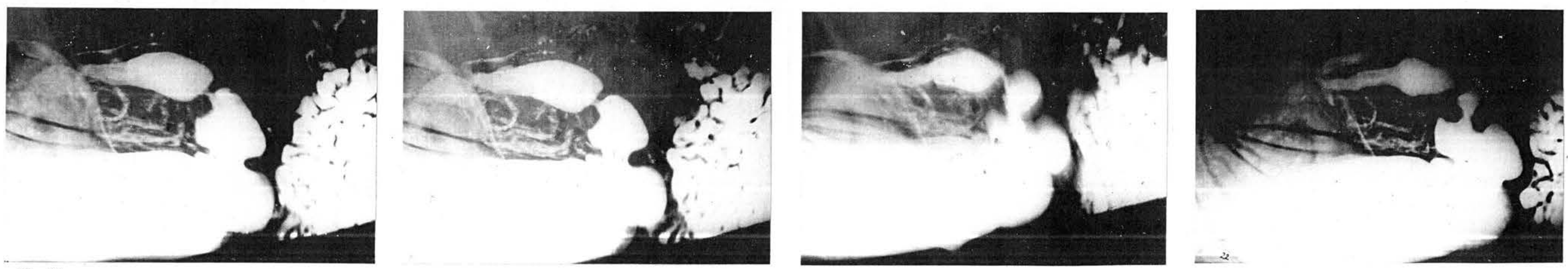

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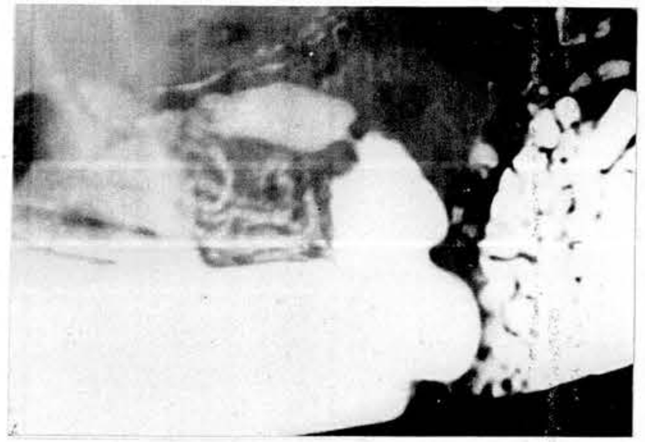

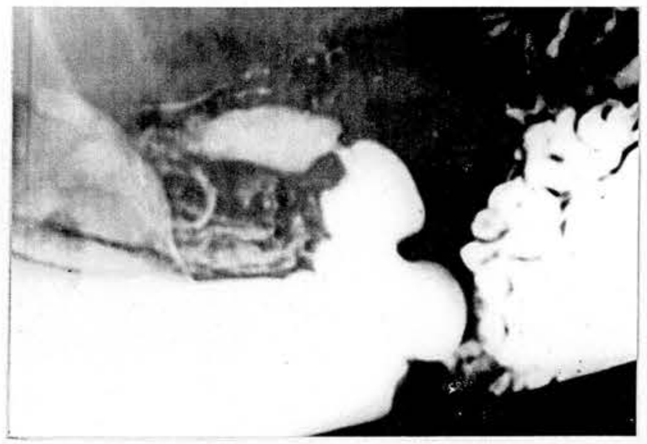
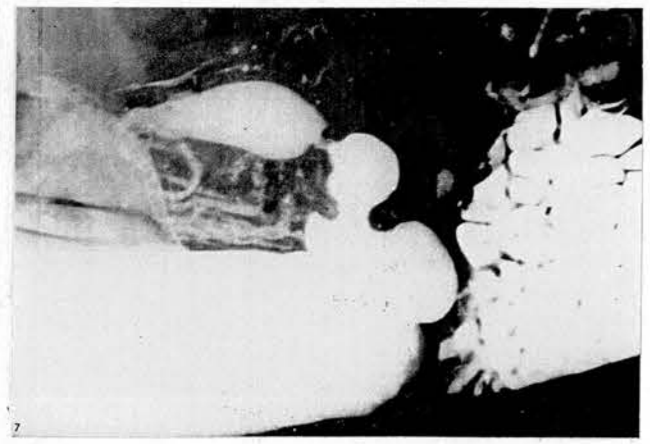
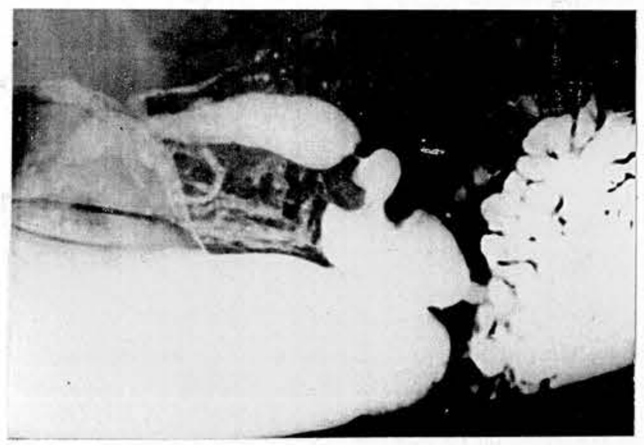
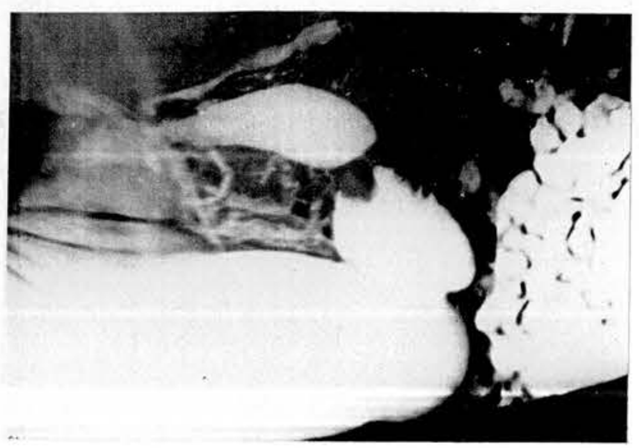
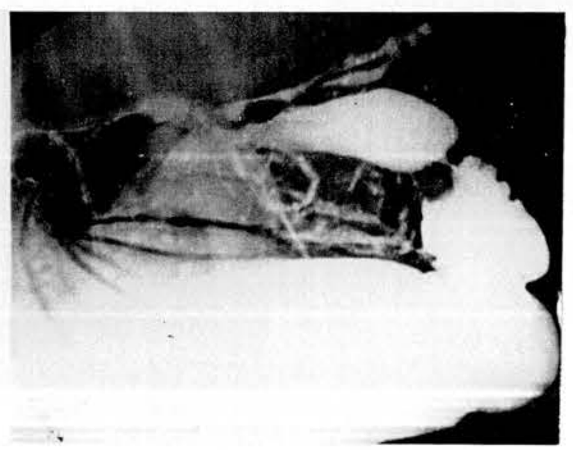
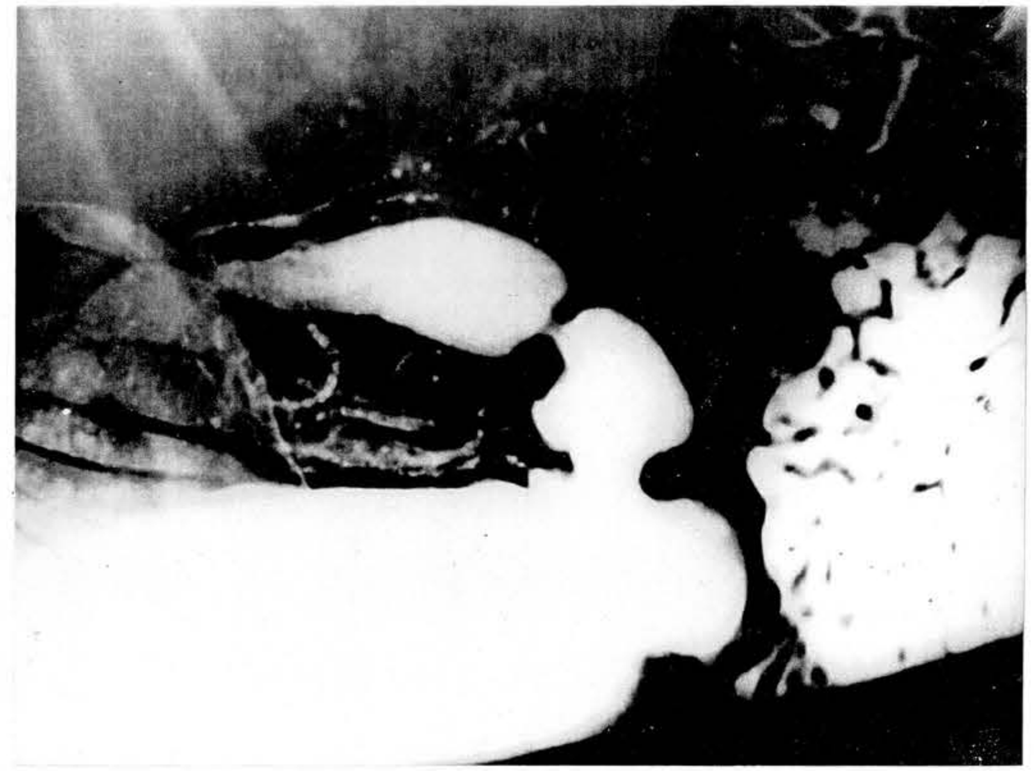

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Plate 7.

Figure 63. Abomasal activity.

The subject was that shown in the previous plate and the series was obtained 30 minutes after the former films. The series consists of 24 frames and was exposed within 48 seconds; the frame interval is 2 seconds.

The abomasum retains the major part of the meal but a considerable fraction is already in the small intestine.

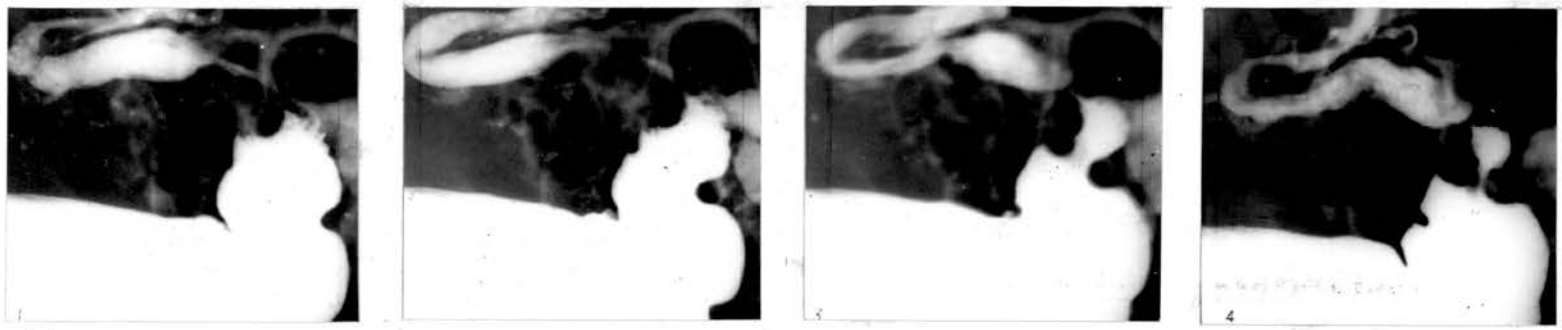
The configuration of the abomasum suggests an orthotonic state of the muscle of its wall. A series of peristaltic waves arise at intervals of approximately ten seconds and are first apparent about the junction of corpus and pars pylorica. Each is at first visible upon the greater curvature, which it only slightly indents, but as it travels distally it becomes more prominent as a sharp incision of this curvature; towards the pylorus it becomes both deeper and wider and where it delimits the pyloric antrum the deep impression it produces is approached by a corresponding but less well defined interruption of the opposing margin. The subsequent fate of the antrum may be studied in the first few frames.

The antrum is limited orally by the peristaltic wave and it will be observed that this lies considerably nearer the pylorus on the lesser than on the greater curvature. In the next two frames the indentation deepens and widens and appears to extend further distally but whether this is due to a movement of the wave or to an extension of the contracted zone and a simultaneous shortening of the antrum cannot be determined. At all events it leads to a fusion on the lesser margin of the indentation of the wave with that of the torus (frame 3): in consequence the now reduced cavity appears to bulge asymmetrically from the greater curvature. Further contraction of the circular fibres leads to the appearance in frame 4: here the antrum forms a narrow canal which is joined distally to the thread-like pyloric orifice which, after relaxing in frame 2, is again contracted.

By the time the antrum has been considerably reduced a new and similar formation has been marked out more proximally and this proceeds to the same fate as its predecessor. Each peristaltic wave requires some twelve seconds to reach the 'preantral' ring and the resulting antral cavity requires a further eight or ten seconds before it disappears - each wave of activity thus endures for upwards of twenty seconds.

At the commencement of the series the duodenal bulb is outlined and is obviously laterally compressed: the pylorus is closed and remains so during the first systole, opening intermittently however during the second (frames 7, 8) during which time the duodenal contents appear to have been reinforced if the density of the shadow is a guide. The pylorus is again open in frames 12, 16 and 17, and also in 19 and 20, and as each relaxation occurs this is followed by an increase in the density and ultimately of the dimensions of the bulb. It will be noted that on each occasion the opening of the pylorus has been of short duration - certainly less than six seconds and more probably of half this period - and has occurred after the commencement of systole but terminating well before total contraction. The increase in the duodenal contents is first accommodated by a transverse expansion, later by a longitudinal extension which is apparently brought about by a general increase in the tone of the circular muscle. More active movement of the duodenum is not noticeable until frames 21 and 22 and is unrelated to the antral activity.

Two or three frames demonstrate movement of the kid: the bleating which accompanied the struggle recorded in frame 21 has produced a herniation of the abomasum through the umbilical foramen. The minor indentations of the antrum in frames 23/4 are possibly due to contraction of the muscularis mucosae.



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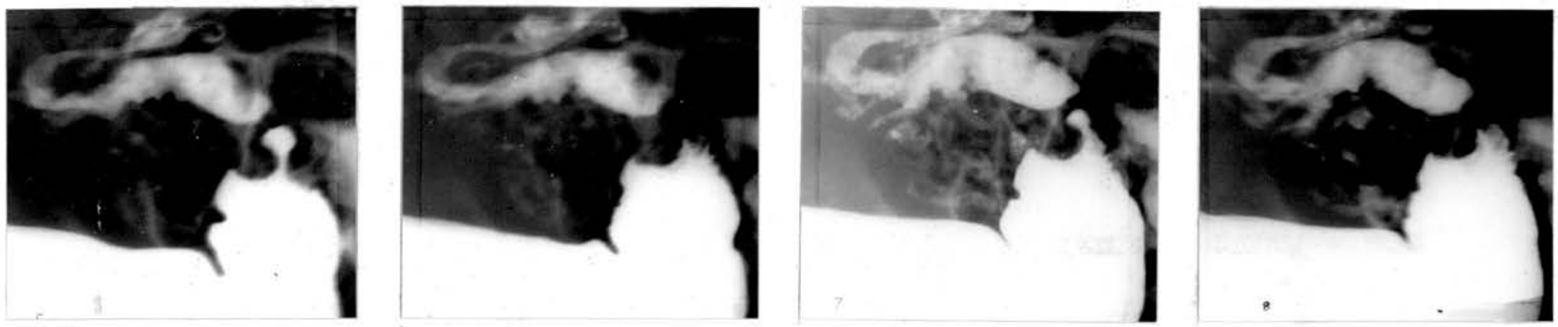

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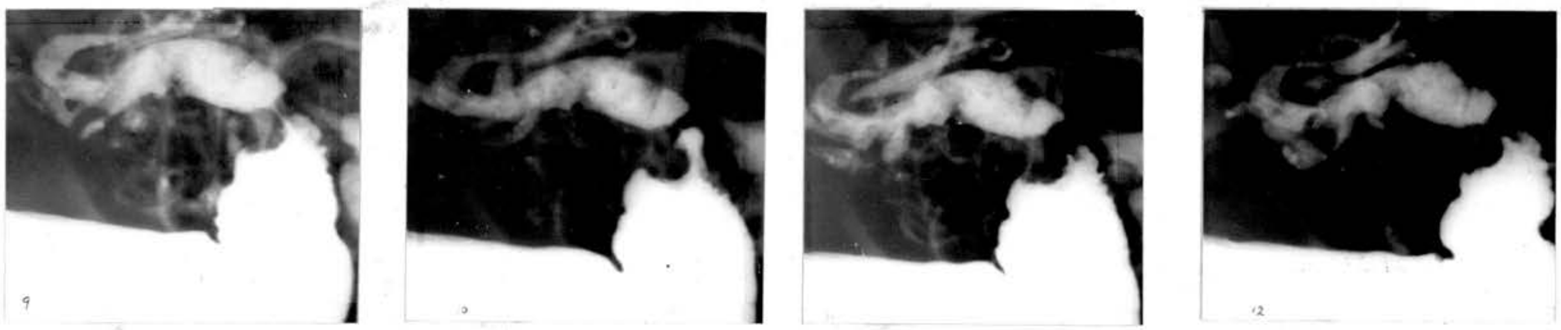

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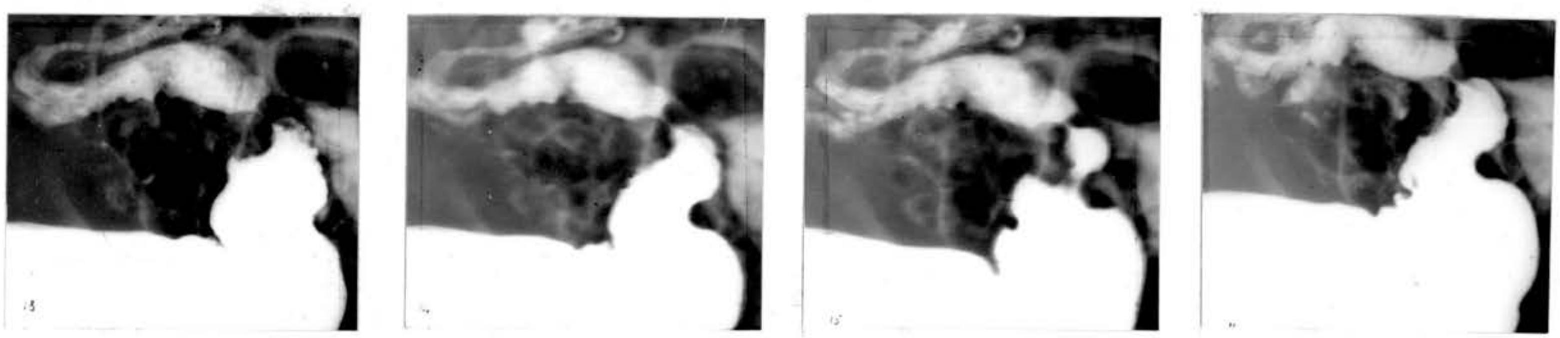

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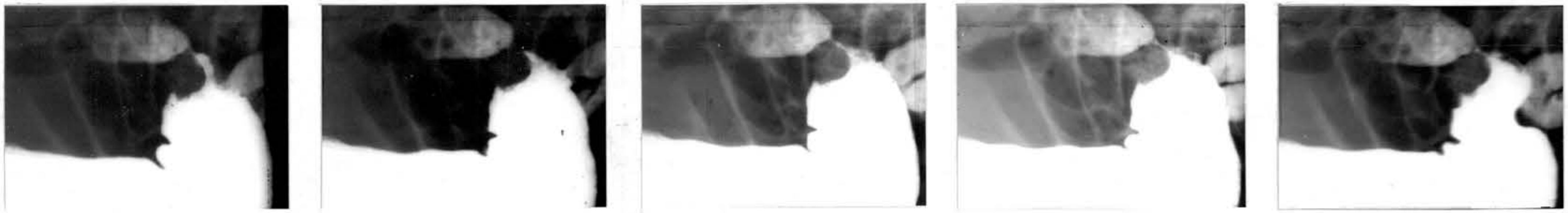
1-5

6-10



11-15

16-18

Plate 8.

Figure 64. Antral systole with slight peristalsis.

This series was obtained from the same subject as that depicted on the following plate. Some peristalsis is evident and the movements of the antral region assume a rather curious form.

The first five frames portray antral systole and on its completion a peristaltic indentation marks off a new 'antrum'. But this does not progress in the usual way: the contraction disappears and the segment against the pylorus opens up by relaxation as in the following series: a period of alternate contractions and relaxations of this region supervenes at this stage before eventually, in frame 12, the new cavity is demarcated. This now proceeds to systole in its turn and in the last frame this also appears to be followed by a wave of relaxation.

This series and the next emphasise the variable relationship of the systolic and peristaltic contractions.

Plate 9.

Figure 65. Antral systole without peristalsis.

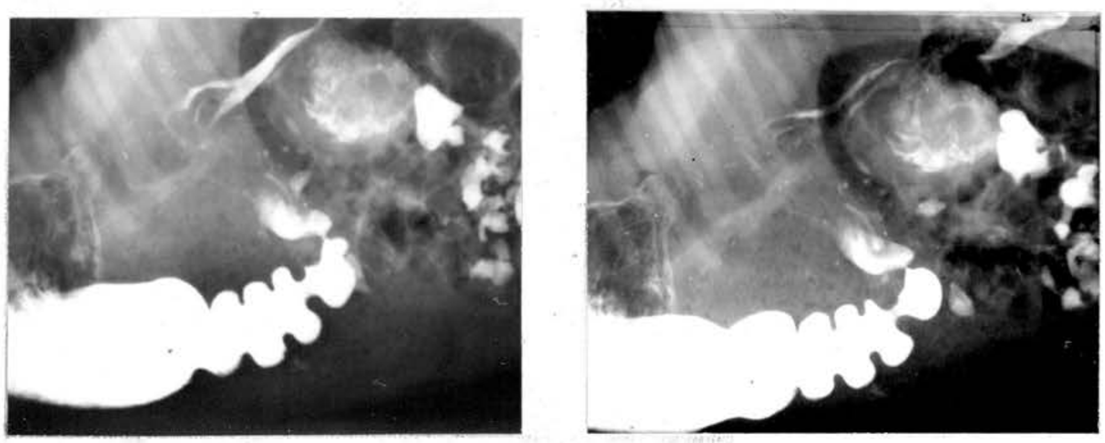
The subject was aged three weeks and the series was exposed three hours after feeding. The sequence covers 34 seconds and the frame interval is two seconds.

This series shows alternate diastole and systole of the pyloric antrum in an otherwise almost inert abomasum. Systole recurs every eight or ten seconds and since there is little peristalsis there is, in place of the succession of antra streaming distally, a slow relaxation of the contracted segment, the wave of relaxation extending from the proximal extremity of the torus pyloricus. Thus the cavity facing this obstruction assumes a pointed form in relaxation in distinction to the more tubular appearance which denotes increasing systole. The development of systole requires 4-6 seconds while the period of relaxation endures for a slightly shorter time: it is however impossible to define these stages exactly since they are separated by periods of suspended animation.

There is no passage of ingesta and the pylorus remains closed during the period of the extract. The duodenal bulb is partially filled and shows, e.g. frames 7-10, slight activity but little or no forward movement of its contents. A loop of small bowel which extends from the right margin of the frames and overlaps the pars pylorica is the site of repeated segmental contractions.

17–19

20–22



23–24

Plate 10

Figure 66. Hyperperistalsis of the abomasum.

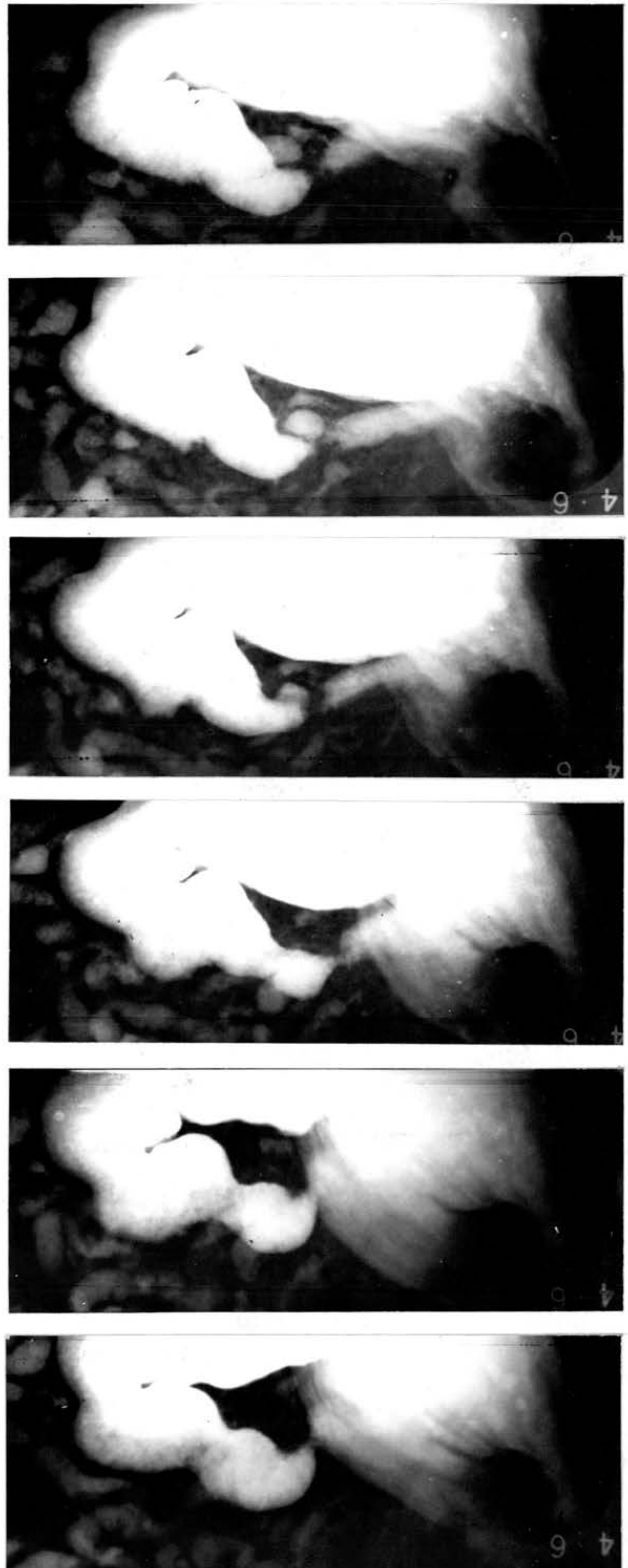
Subject aged 32 days examined 2 hours 45 minutes after feeding. The duration of the complete series of 24 frames was 28 seconds, the frame interval is thus approximately $1^{1}/6$ second. The period covered by the extract is 9-10 seconds.

The greater part of the meal remains in the abomasum but a fraction has passed on to the more distal part of the small gut and traces have entered the caecum and proximal part of the colon.

The abomasum is hypertonic and exhibits peristalsis of unusual intensity. The peristaltic waves, of which four or five are seen in passage at a time, arise as shallow and wide indentations of the distal part of the body and are almost equally well marked on the two curvatures. On reaching the pars pylorica they greatly increase in depth and they continue to deepen as they approach the pylorus. They are somewhat modified as they advance over the immediately prepyloric region and the appearance is again created of a succession of 'antra'. Each wave is visible for about 12-14 seconds of which 4-5 seconds cover the formation and contraction of the terminal cavity or antrum - a considerably more rapid sequence than in certain of the series previously studied.

It will be noted that the pylorus is closed in some frames (e.g., 18), and open in others (e.g. 26).

Relaxation of the pylorus appears to coincide with the middle period of the life of the antrum and while separation of this cavity from that of the immediately proximal segment of the abomasum is never complete it appears likely that small amounts of the milk are ejected into the duodenal bulb during some, at least, of the antral contractions. The duodenum is active about the middle of the sequence and in frame 21 the bulbar contents have been expelled into the succeeding section: in the next frame this shadow has split into two parts, one of which has partially refilled the bulb while the other, more distal portion, continues through the duodenum.



1-6

Plate 11.

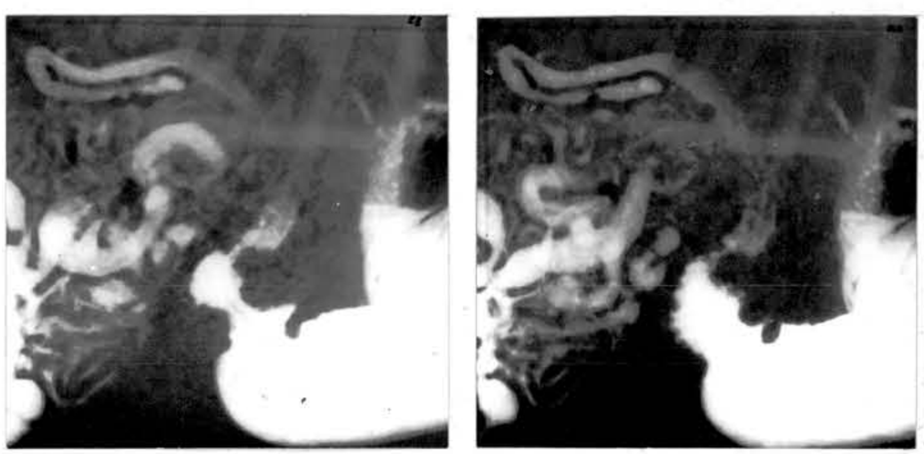
Figure 69. Abomasal activity in the older kid.

Subject aged 8 weeks, series obtained 2 hours 10 minutes after feeding. Frame interval $1\frac{2}{3}$ seconds.

The movements portrayed in this series typify those of the rather older kids (see also fig. 68). The peristaltic waves are slow moving and vary in their amplitude and intensity as they proceed distally. There appears to be a more extensive contraction at the narrow antrum and this may be regarded as an incomplete systole of this part. As usual the pylorus is open during the intermediate phase of contraction (frame 3) and closed later. It is impossible to determine whether there is any ejection of the abomasal contents at this time.

13-17

18 - 22



23-24

Plate 12.

Figure 75 . Duodenal activity.

The subject was aged six weeks and the series exposed 2 hours after feeding. The complete series consisted of 24 frames: the first twenty were exposed at 2 second intervals: there then occurred a delay of 30 seconds before the remaining frames (the last four reproduced) were exposed. These also are separated one from another by an interval of 2 seconds.

Most of the meal remains in the abomasum. The duodenum is unusually full and much of the small intestine is also outlined. A small amount of the opaque material had reached the caecum.

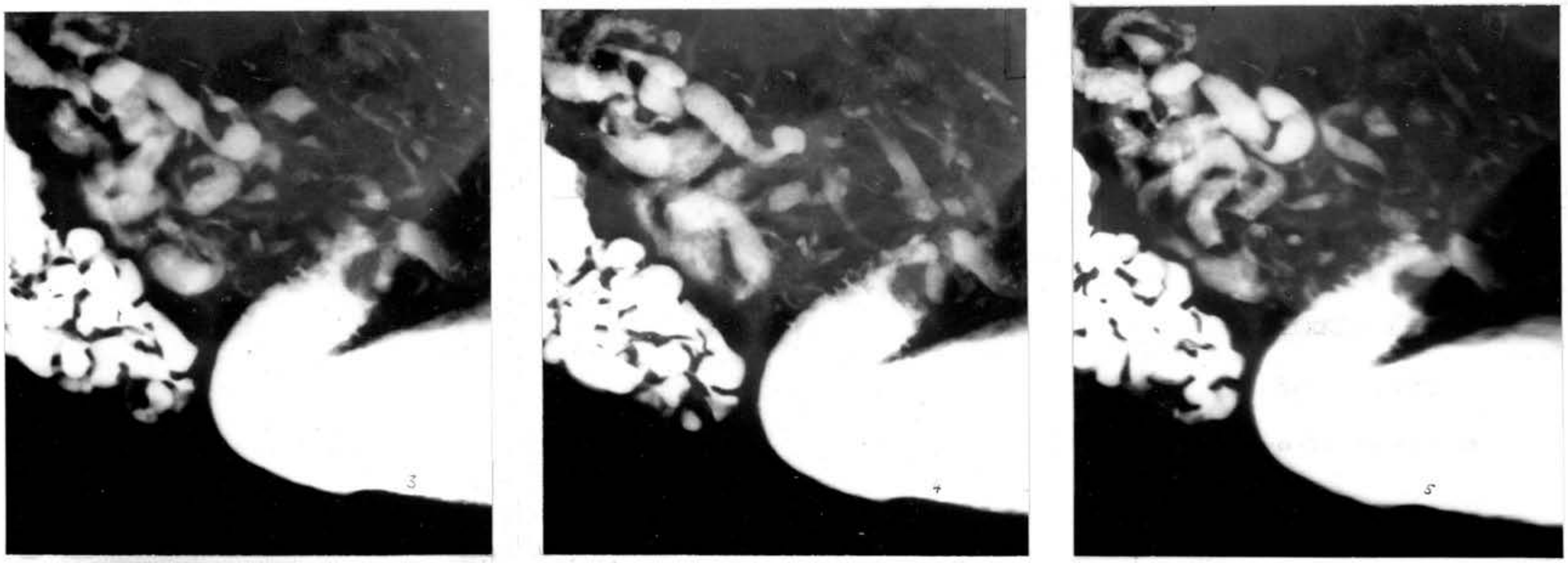
The abomasum possesses a rather unusual form for a kid so old and its appearance suggests hypertonicity. The full series and the preceding and subsequent screening observations showed that irregular peristaltic waves, confined to the pars pylorica, travelled distally and gave way to antral systoles which were accompanied by almost complete separation of the distal segment. For the most part the systole was followed by a relaxation and period of repose before the development of the next contraction and the appearance was quite different to that obtained when more regular peristalsis results in the formation and flowing of a series of dilatations: however alternations of this form of movement did occur during the fifteen minutes of continuous observation which preceded these films. Numerous minor indentations of the abomasal contours are probably due to the contractions of the mucosal muscle and these, it will be observed, may persist during the systole.

The principal interest of this sequence lies in the duodenum. This part of the intestine shows several unusual features - a comparatively narrow and ill-defined bulb, the absence of a portal convolution and occupation by an almost continuous column of ingesta. During the preliminary screening the bulb showed conspicuous alternations of contraction and elongation, each cycle enduring for 3-5 seconds but these are not evident in the series.

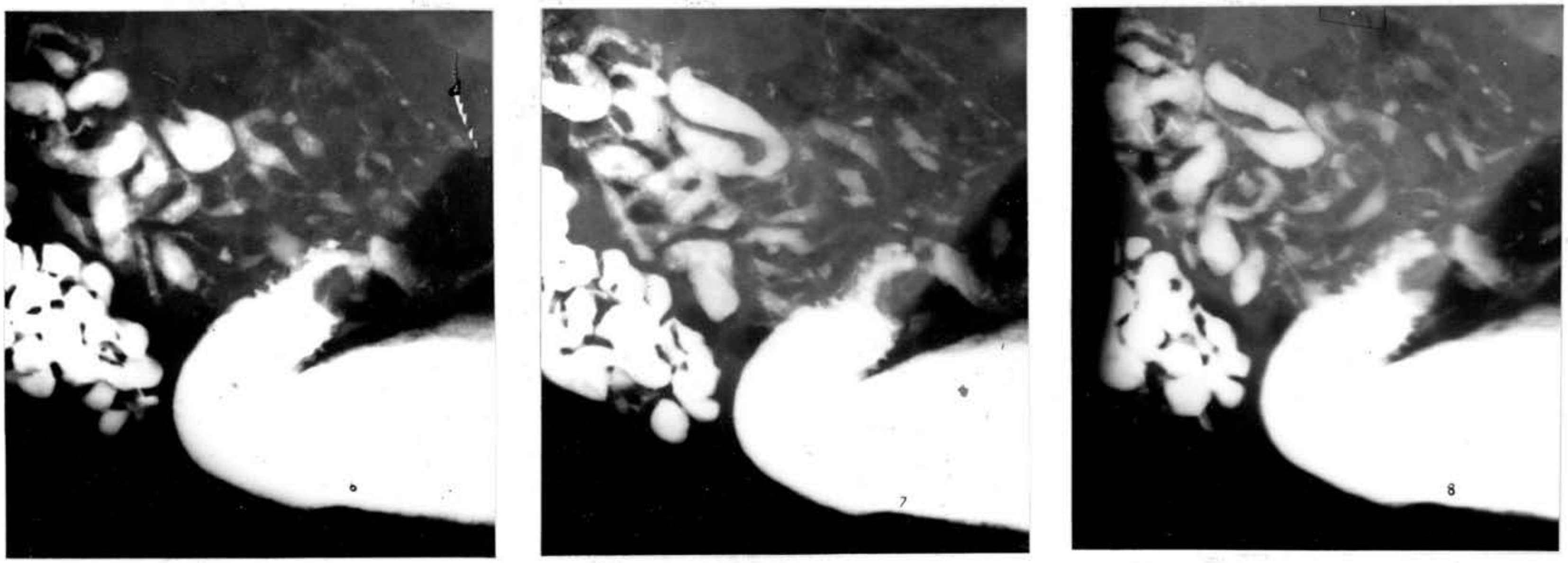
In frame 1 the bulb is largely collapsed and the irregular distribution of the ingesta shows that the section of the lumen varies, at one point a little beyond the pylorus, apparently resembling a 'keyhole' in section. More distally there are long contracted segments alternating with more expanded regions. Their appearance has quite altered during the two seconds that separate the next view: here the base of the bulb is quite obliterated - witness the increased interval between the abomasal and bulbar shadows - and when the lumen opens more distally there is a small dilatation followed by a larger zone of contraction: beyond this is an extensive widened part tapering off distally and exhibiting a long tail.

The next two frames more closely resemble the first but there is a continual activity along the distal segment and a shunting of the material to and fro. The later frames merely repeat these processes in a continuously varying form and it will be noted that despite this great activity there is very little advancement of the head of the column along the ventral limb of the duodenal loop.

The position is somewhat obscured from frame 19 onwards by the passage of a large 'bolus' through the complicated convolutions of the jejunum which carry it across the course of the duodenum.



3-5



6-8

Plate 13.

Figure 77 . Small intestine activity.

Subject aged 4 weeks, 2 hours 45 minutes after feeding. The frame interval is 2 seconds.

As has been explained in the text the complex coils of the small intestine of the ruminant and the short columns of the ingesta are not favourable to serial study. These few frames do however show something of the changes that occur and attention is particularly directed to those loops of moderate density lying in the top half of the picture, to the left of centre.

It will be seen that the column is irregularly divided by a series of incomplete segmental constrictions which disappear and reform more rapidly than the exposures record, and it will be noted that these contractions are accompanied by a gradual movement of the material along the bowel.

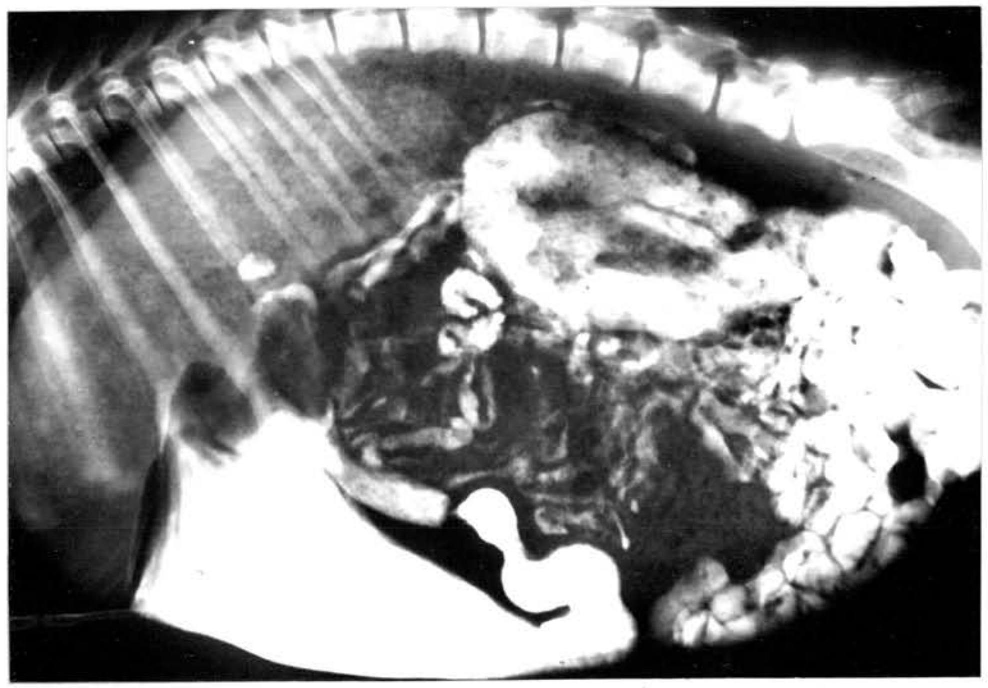
The smaller streaks to the right are either more rapid in the execution of their movements or else, as is the case with the horseshoe loop seen in frames 5 and 6, they remain quite stationary for periods.

More detailed interpretation is impossible.

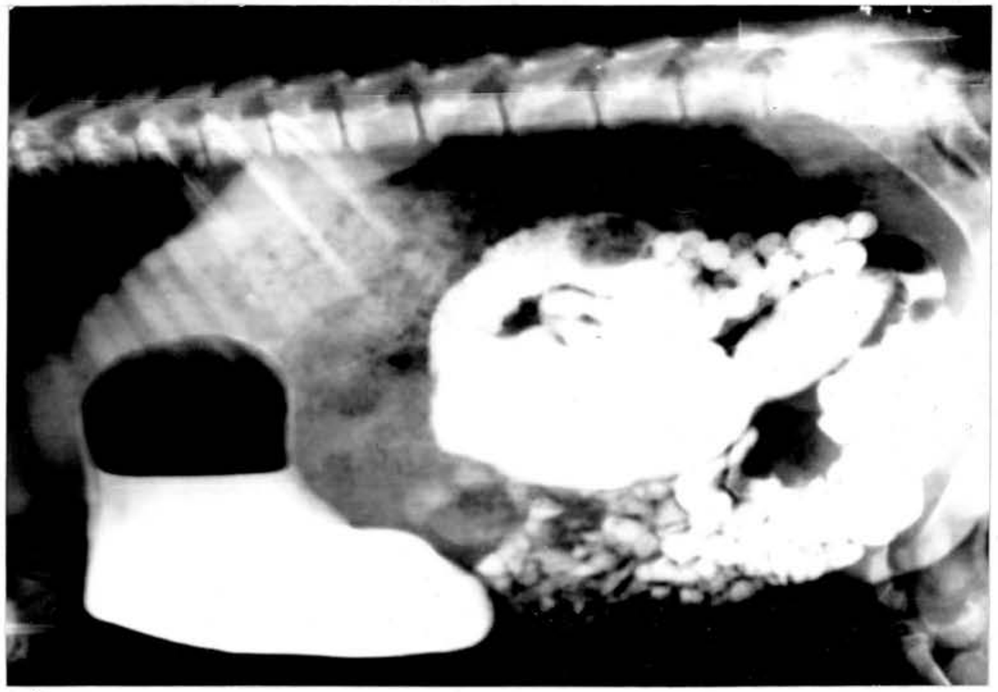
A

C

B



D



E

F

GUIDE to LOCATION of FIGURES

Plate 14.

Figures 88 A - F. The passage of a meal through the tract.

This sequence of films is included to give a general notion of the passage of a single meal through the tract. The kid was aged 8 weeks.

Fig. A. Ten minutes after feeding.

The milk meal has coagulated and lies in the abomasum which shows slight activity with the development of a contraction at the level of the incisura angularis. A trace of the feed remains in the omasum and small quantities have already reached the duodenum.

Fig. B. Two hours after feeding.

The abomasal tone is increased. Most of the meal remains in the abomasum and of that fraction which has escaped the greater part is 'clumped' in the distal part of the small intestine.
(Fig. 69, plate 11 follows at 2 hours 15 minutes).

Fig. C. Two hours 30 minutes.

There is little change in the disposition of the meal. The duodenal bulb is exceptionally well delineated.

Fig. D. 4 hours 30 minutes.

Considerably more of the meal has passed into the intestine. The caecum and ansa proximalis are well shown and a large part of the small intestine is engorged.

Fig. E. 6 hours 30 minutes.

Little more has left the abomasum. The caecum, proximal and spiral coils of the colon are all filled.

Fig. F. 27 hours.

The abomasum and small intestine are empty but the entire large intestine is full. The large bowel was not cleared until some time between the 48th and 53rd hour.

FIGURE	FACING PAGE	FIGURE	FACING PAGE
1	2	51 & 52	106
2	28	53	107
3	29	54	108
4	39	55 & 56	109
5	40	57	110
6 & 7	41	58	111
8	238	59	112
9	54	60	113
10	55	61	114
11	56	62	255
12 & 13	57	63	256
14 & 15	58	64	259
16	59	65	260
17 & 18	60	66	261
19	61	67	123
20 & 21	62	68	127
22 & 23	63	69	263
24	64	70	148
25 & 26	65	71	149
27	66	72 & 73	150
28 & 29	67	74	162
30	68	75	264
31	76	76	164
32	241	77	267
33	249	78	-
34	251	79	173
35	83	80	174
36 & 37	84	81	175
38	90	82	176
39	252	83	177
40,41 & 42	97	84 & 85	178
43	98	86	188
44	99	87	190
45	101	88	268
46	102		
47	103		
48	104		
49 & 50	105		